

STUDIES ON MESOZOIC AND CAINOZOIC
DINOFLAGELLATE CYSTS



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By R. J. DAVEY, C. DOWNIE,
W. A. S. SARJEANT & G. L. WILLIAMS

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SYNOPSIS

The morphology of fossil dinoflagellate cysts is discussed ; the cysts are shown to fall into three broad groups (" proximate ", " chorate " and " cavate "), which are interpreted as indicating different modes of formation. New terms are proposed, to enable more precise description of cyst morphology. The principal genera are reconsidered, in the light of new information from studies of assemblages from the Cretaceous (Speeton Clay and Chalk) and Eocene (London Clay) of England. 27 new genera are proposed and emendations are given to the diagnoses of 16 existing genera ; 64 new species are described and the diagnoses of nine existing species are emended. In addition, the generic allocation of other species already

described, from all stratigraphic levels in the Mesozoic and Cainozoic, is reviewed and generic transfers are proposed where necessary. The resultant picture of the stratigraphic distribution of genera and species emphasizes the value of these microfossils as stratigraphic indices.

I. INTRODUCTION

DURING the last few years, research into the nature and distribution of fossil dinoflagellate cysts has been very active, stimulated by realization of the potential value of these microfossils in the correlation of marine strata and by their biological interest. The great bulk of recent researches has been made by French and German palynologists, notably Deflandre, Valensi, Eisenack and Gocht.

In Britain, a brief period of interest followed Ehrenberg's initial discovery of these fossils in flints and his visit to England in 1838: however, after 1850, no further attention was paid to these fossils for a century. In 1957 Downie described a number of types from the Upper Kimmeridge Clay (Kimmeridgian): this was the first study of British Jurassic dinoflagellates. Subsequently Sarjeant, in a series of publications, has described assemblages from the Cornbrash, Oxford Clay, Corallian and Ampthill Clay (Callovian to Oxfordian): species described by this author (1962) from the Cotham Beds (Rhaetic) include the earliest known clearly tabulate cysts. The distribution of dinoflagellate cysts in the Lias has been studied by Wall (1965).

The first British Lower Cretaceous assemblage to be described was from the Hauterivian section of the Speeton Clay (Neale & Sarjeant 1962), species from other levels of the Speeton Clay are described herein. An assemblage from the Cambridge Greensand (Middle Cretaceous) has been described by Cookson & Hughes (1964). Since 1850, no further work has been published on the Upper Cretaceous: the first results of studies by Davey, at present in progress, are included in the present work.

No British Tertiary assemblages have yet been described. Dinoflagellate cysts from the London Clay (Eocene) have been mentioned by Eagar & Sarjeant (1963) and figured by Mackó (1963), but the first extended study was that made by G. L. Williams (thesis, 1964), of which results are given herein.

No Quaternary assemblages have been described; work by Deflandre referred to by West (1961) has not been published.

There has been considerable progress in recent years in our understanding of the nature of these cysts, largely as a result of the studies of Evitt (1961, 1963, Evitt & Davidson 1964). He has elucidated some of their fundamental structures and drawn attention to the importance of the cyst openings (archaeopyles) and of structures representing a reflected tabulation, thus effectively demonstrating the affinity of many formerly problematic genera (the "hystrichospheres" *sensu stricto*).

This paper comprises a full-scale review of certain of the principal genera of fossil dinoflagellate cysts, involving extensive revision of generic diagnoses and the erection of new taxa. In addition, new genera and species are described from various Mesozoic and Tertiary horizons.

II. THE MORPHOLOGY, TERMINOLOGY AND CLASSIFICATION OF FOSSIL DINOFLAGELLATE CYSTS

By C. DOWNIE & W. A. S. SARJEANT

In the description of fossil dinoflagellates in the past, the terms used have been largely borrowed from modern plankton descriptions. This is appropriate enough : however, as studies of fossil dinoflagellates have developed, structures have been discovered for which no terms exist and the use of descriptive terms, without specification of precise meanings, has produced, on the one hand, ambiguity, on the other hand, the failure to distinguish between different, albeit broadly similar, structures—cf., for example, past usage of the terms “ spine ” and “ tube ” in description of appendages.

The work of Evitt (1961, 1965, in press) has gone some way towards the establishment of precise terms for some morphological characters. In the present work, a number of new terms are proposed which, it is hoped, will form a workable basis for future descriptions.

In addition, the existence of broad groupings of morphologically similar dinoflagellate cysts has become apparent : these groupings appear to have considerable stratigraphic meaning. The classification at present in use is criticized for not taking cyst structure into account.

MORPHOLOGY AND TERMINOLOGY. (1) Cysts and Motile Stage Thecae.

Evitt & Davidson (1964) have described the process of cyst formation in some Recent dinoflagellates and have shown that these resting cysts are of types closely resembling some of the most common fossil species. They conclude that most, if not all, of the fossil remains of dinoflagellates are cysts. These cysts are smaller than the motile stage cell and are formed by the deposition of an ellipsoidal or spherical wall some distance inside the motile stage envelope (or theca if hardened). This wall in fossil and Recent cysts is often seen to be constructed of two layers, which we propose to call the endophragm and the periphragm. The outer layer, or periphragm, usually carries extensions, either in the form of spines or as lists, which extend out to the position of the formal thecal wall and appear to have acted as supports during the period of cyst formation (Text-fig. 1).

Many kinds of fossil dinoflagellate cysts are equipped with a special opening which functions when the cyst contents are to be released. These openings, called archaeopyles by Evitt, generally have a definite polygonal shape and are fixed in location in any particular species. Their presence in a fossil demonstrates that it is a cyst. Fossil remains of potentially motile dinoflagellates lack an archaeopyle and have a cingulum, or transverse furrow, in the form of a continuous spiral groove which has no impediments such as spines and septae crossing its track, indicating that this was the former position of the transverse flagellum (Text-fig. 2).

Tabulation, which is a striking feature of the living armoured dinoflagellates, can also be represented in cysts, often highly modified, but its presence or absence is not determinative in distinguishing cysts from motile stage thecae.

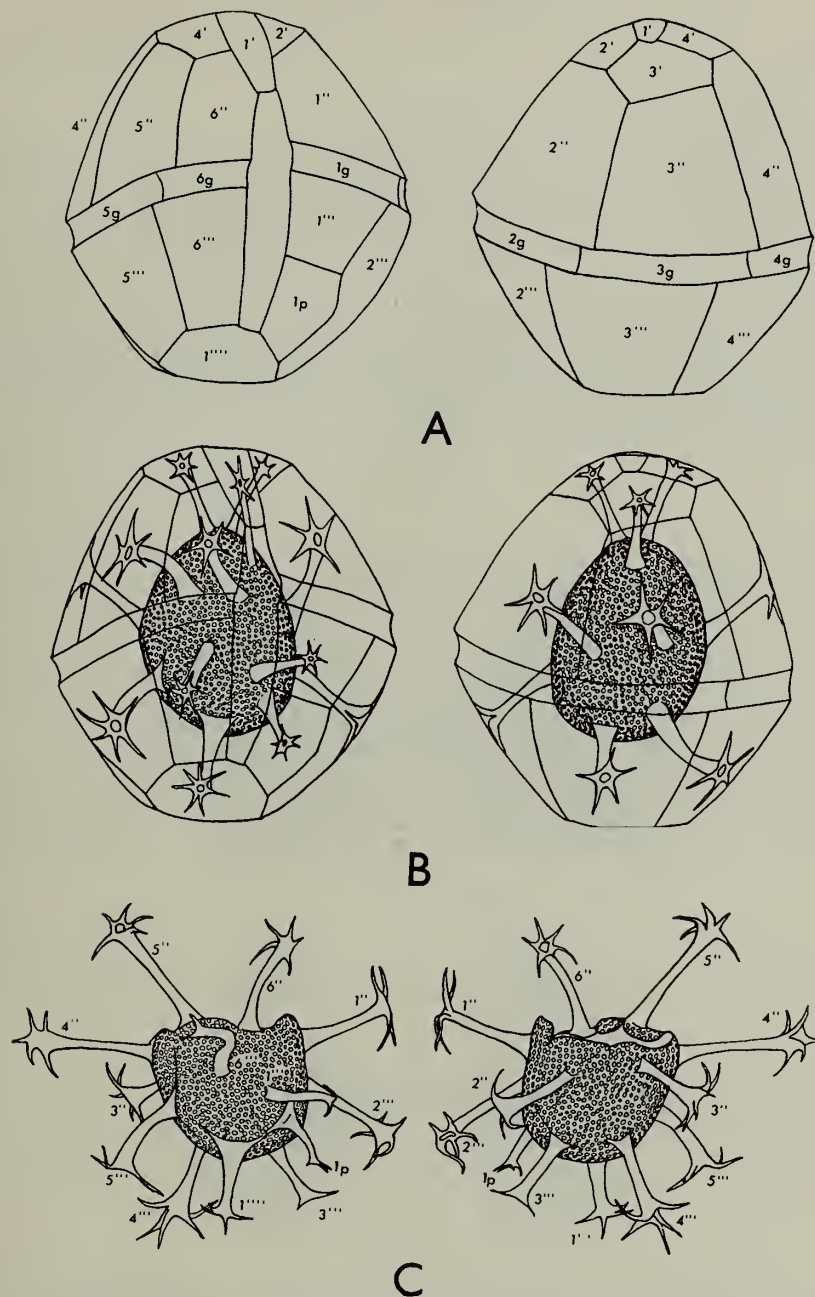


FIG. 1. *Oligosphaeridium vasiforme* (Neale & Sarjeant), a typical chorate cyst, showing the presumed method of cyst formation. A, The probable original tabulation of the dinoflagellate, which corresponds to that of *Gonyaulacysta*. (The apical tabulation is wholly speculative.) B, The cyst forming within the dinoflagellate theca, attached to the cell membrane by its processes. C, The abandoned cyst as found, with an apical archaeopyle. [After Sarjeant (1965) reproduced by permission of the Editor of "Endeavour".]

The term "ambitus" applied to dinoflagellates refers to the test outline viewed from the dorsal or ventral side.

(2) The Morphology of Motile Stage Thecae.

Modern dinoflagellates may be thin-walled or may have robust cellulosic tests (thecae), which are clearly divided into fields by sutures in the tabulate genera. Text-fig. 2A shows a test of this type and indicates the terminology used to describe it. Other morphological structures are shown in Text-figs. 3, 4.

(3) Fossilized Motile Thecae.

Very few fossil dinoflagellates could be considered as the remains of motile stage thecae. The strongest claims can be made for some species of *Peridinium* and *Gymnodinium* from the Upper Cretaceous which lack archaeopyles and show no other structures characteristic of cysts.

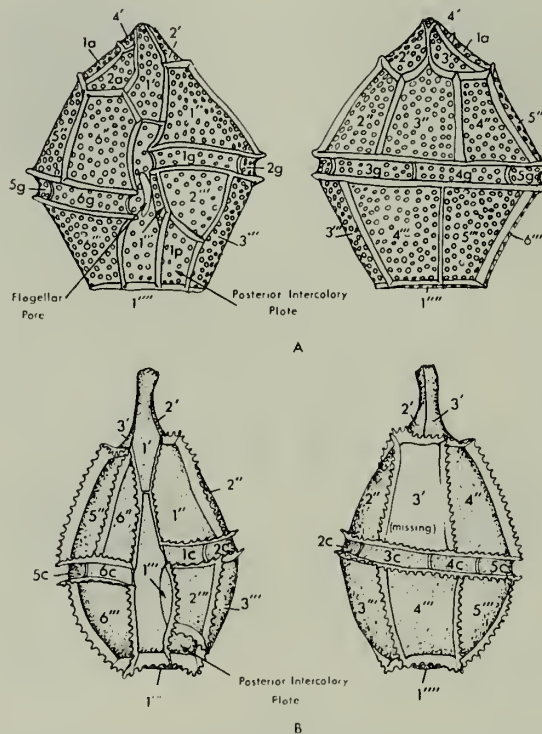


FIG. 2. The tabulation of a modern dinoflagellate, compared with that of a proximate dinoflagellate cyst. A, *Gonyaulax polyedra*, a dinoflagellate of present day warm and temperate seas. After Kofoid. B, *Gonyaulacysta jurassica*, from the Upper Jurassic; a proximate cyst with a precingular archaeopyle. [After Sarjeant (1965) reproduced by permission of the Editor of "Endeavour".]

(4) The Morphology of Cysts.

(a) *Major Cyst Types.*

The cysts are always smaller than the motile cell and can be grouped according to their degree of contraction. The degree of contraction also affects their general appearance, for those which are most condensed bear little superficial resemblance to the parent cell, whereas those that are near the motile cyst in size closely resemble it in appearance. Consequently two groups of cysts are here recognized, the *chorate* (or condensed) cysts and the *proximate* cysts.

In both these groups of cysts, the two wall layers are generally in close contact and only rarely come apart, but there is a third group, here called the *cavate* cysts, in which a space, or spaces of notable size, occurs between the periphragm and endophragm. This space is here named the pericoel; it separates an inner body (capsule) formed by the endophragm from the outer cyst wall, the cavity of this inner body is called the endocoel.

(b) *Cyst Openings.*

The polygonal openings found on cysts have been called pylomes by Eisenack. This is, however, a broad term and includes also circular or slit-like openings which are in no way characteristic of, or confined to, the dinoflagellates. Evitt's term archaeopyle refers specifically to those kinds of pylome which characterize some dinoflagellate cysts. They are usually polygonal and precisely located and orientated on the test, corresponding to specific locations in the structure of the *tabulate* dinoflagellates. The terminology used here generally corresponds to that proposed by Evitt (1961, text-figs. 5-8), with the addition of *epitracial*, for archaeopyles formed by breakage parallel, and immediately anterior to, the cingulum (equivalent to *epithecal* archaeopyles of Norris 1965), and *cingular*, for archaeopyles formed by

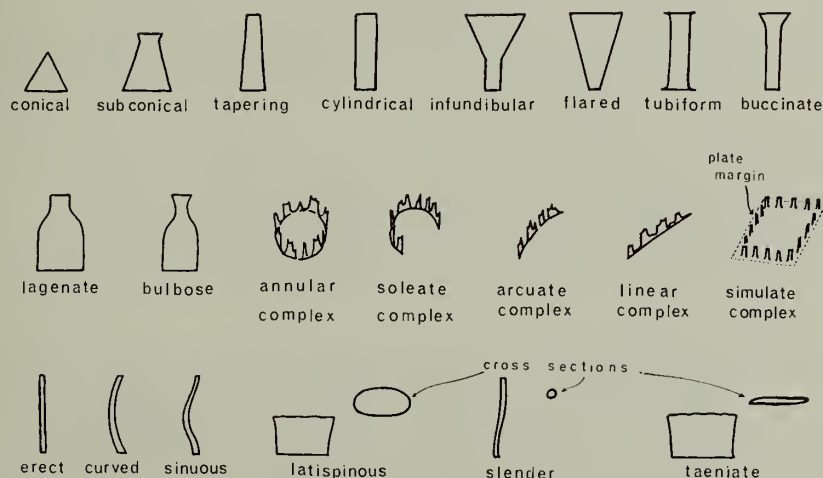


FIG. 3. Illustrations of the terms used to describe the overall shape of the processes and process complexes. The distal end is uppermost in each case.

breakage along and within the cingulum. Apical archaeopyles are called *haplo-tabular* when they consist of a single plate and *tetratabular* when they have four.

(5) Proximate Cysts.

The proximate cysts are an important group, which have always been recognized as dinoflagellates because their resemblance to modern forms is very close. Nevertheless, although all the features of tabulation may easily be determined on good specimens, they are not motile thecae, but cysts. The terms epitheca and hypotheca used for motile stages, are therefore inappropriate. It is here proposed that their cyst equivalents should be termed *epitract* and *hypotract*, names suggested by G. L. Williams (thesis, 1964).

Contraction in the formation of the proximate cyst is generally to about $\frac{1}{2}$ or $\frac{2}{3}$ of the original volume; this can roughly be gauged by the height of the periphragm spines or lists. The ratio $\frac{\text{Radius of endocoel}}{\text{Radius overall}} = 0.8$ constitutes a rough limit to the proximate cysts.

The periphragm often forms extensions which bear a close relationship to the presumed tabulation of the motile stage theca. These extensions are nearly always sutural (i.e. reflecting the site of the sutures on the motile stage) and most often consist of continuous crests or lists, often with serrate or denticulate edges. Less commonly, lines of small solid spines or tubercles mark the reflected sutures.

Subdivision of the proximate group of cysts is based on a number of features among which the reflected tabulation, the overall shape of the test (i.e. elongation, number of horns) and the nature of the archaeopyle are important.

Typical of the proximate cysts is the genus *Gonyaulacysta*. The group as a whole is more characteristic of Upper Jurassic–Lower Cretaceous than of later strata.

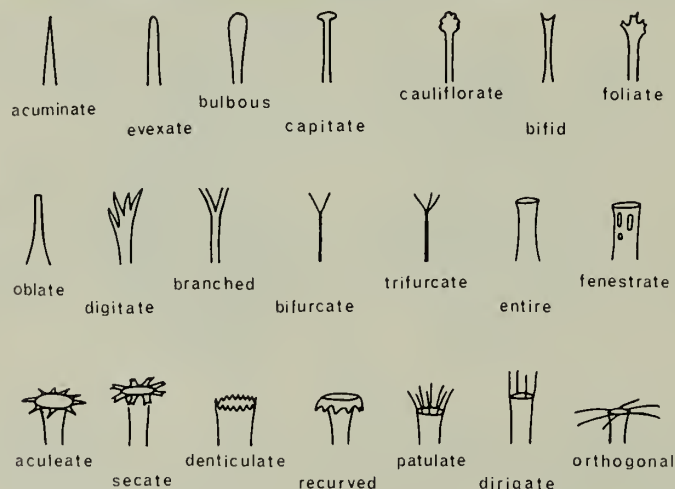


FIG. 4. Illustrations of the terms used to describe the various kinds of distal termination of the processes.

(6) Chorale Cysts.

Chorate cysts in general resemble *Hystrichosphaeridium* and include all the typical hystrichospheres. They are distinguished from proximate cysts by the greater contraction that took place during cyst formation, for the cyst has only about $\frac{1}{3}$ the volume of the motile cell and the contraction ratio $\frac{\text{Radius of endocoel}}{\text{Radius overall}}$

is typically about 0.6. As a consequence of this greater contraction the tabulation is often only indirectly determinable, if at all, and the general appearance is not dinoflagellate-like. Furthermore, the outgrowths of the periphragm are longer and often exceed in length the endocoel radius. These outgrowths are commonly spine-like, and are either located from the site of the sutures (sutural appendages) or within the edges of the plates (intratabular appendages).

Intratabular appendages occur in various ways, but are usually either hollow or grouped in patterns related to the tabulation. The hollow processes are open at the distal end in *Hystrichosphaeridium*, but in *Cleistosphaeridium* they are closed distally. So far, no species definitely identified as a dinoflagellate cyst has spines which open into the endocoel.

The open-ended processes have various kinds of distal openings, which may flare like trumpets or constrict; various kinds are illustrated in Text-figs. 3, 4. In some cyst groups the processes may be connected distally by narrow solid rods (*trabeculae*): in others a thin membrane (*ectophragm*) may still persist between the distal ends. The ectophragm must have been laid down very close to the motile cell envelope. Often only one appendage occurs on each plate, but there may be more, and when the appendages are very numerous the tabulation may not be determinable at all.

Other kinds of intratabular appendages are often found to be solid and to occur in groups (see Text-figs. 3, 4). *Polystephanephorus* is characterized by annulate groups, and *Areoligera* by coronate and soleate groups. Usually no more than one group is found associated with one plate so that they are useful in determining the tabulation.

Sutural elements may consist of rows of spines or of spines situated only at plate corners (gonal spines), but commonly these spines have merging bases forming continuous flanges or lists as in the proximate cysts. These elements are usually solid but small pyramidal cavities may develop at the base of the gonal spines, which in *Hystrichosphaeropsis* begin to run together to form a larger, more continuous cavity.

Several sub-divisions of the chorale group of cysts are found to be useful. The typical chorale cysts are represented by highly condensed forms like *Hystrichosphaeridium* and *Cleistosphaeridium* with cylindrical or spine-like processes. Their condensation ratio is about 0.5 or 0.6 and the outgrowths are intratabular. Proximate cysts include forms like *Hystrichosphaera* which have generally lower condensation ratios (0.6–0.8) and sutural outgrowths which more readily indicate the tabulation. *Raphidodinium* is a highly condensed representative. The *trabeculate*

chorate cysts are represented by *Cannosphaeropsis*; and *Membranilarnacia* is typical of the *membranate* group.

A *pterate* group can also be recognized with *Wanea* as a representative, its main characteristic being its pronounced equatorial outgrowth in the form of solid processes linked distally or in mesh-like fashion. The *marginate* cysts form a group, typified by *Areoligera*, consisting of chorate cysts whose outgrowths are characteristically localized on the lateral margins, leaving the dorsal and more often the ventral surfaces free of large outgrowths.

Chorate cysts have a very long history, but they are more important in the Upper Cretaceous and Tertiary than at any other time.

(7) Cavate Cysts.

In some forms already mentioned, small pericoels have been found between the endophragm and periphragm. In the cavate group of cysts, the pericoel is a dominant feature, so that the body consists of an inner body (capsule) formed by the endophragm and an enclosing body, formed by the periphragm, often of quite a different shape.

The inner body is usually ellipsoidal, thick walled, with a smooth or granular surface. It may have an archaeopyle but rarely shows any sign of tabulation. In a few forms spinous projections bridge the gap between the endophragm and the periphragm, but in many the cavity is more or less continuous and contact between the two is either not apparent or occurs only at the mid-ventral line. The periphragm is usually thinner and often smooth. It does however quite often have an archaeopyle and may show a tabulation marked by sutural lines, or by intratabular spine pallisades as in *Wetzeliiella*. The overall shape is an important feature in these cysts, especially the number and positions of the horns on the periphragm.

A number of sub-groups are recognized depending on the degree of continuity of the pericoel. In typical cavate cysts like *Deflandrea phosphoritica* there is only one large pericoel extending over nearly all the body. In bicavate cysts there is a wide zone of contact round the equator which divides the pericoel into an apical and antapical part; *Triblastula* is typical of this group. *Stephodinium* represents a small group (the *ptero-cavate* cysts) with a pronounced equatorial pericoel. Small pericoels may occur in other groups such as the apical pericoels in some proximate cysts, the gonal pericoels in some *Hystriosphera* species.

(8) Other Cyst Groups.

In addition to the three main groups discussed so far one must recognize the existence of groups of fossil dinoflagellates with calcareous tests and with siliceous tests. Neither of these groups is being considered in this paper, although most appear to be non-motile and probably encysted.

CLASSIFICATION. Eisenack (1964) published a classification of fossil dinoflagellates which is by far the most comprehensive classification yet attempted. In this paper he adopts a botanical system, which is welcomed. However, his classification

cannot be considered satisfactory, because he does not allow enough importance to the fact that we are dealing with cysts.

Evitt & Davidson (1964), Deflandre (1962) and Norris (1965) have cogently stated the taxonomic problem that arises because so little is known about the encystment of living species of dinoflagellates. Currently the classification of living species and genera is based on the tabulation and appearance of the motile stage cell, but it is now known (Evitt & Davidson 1964) that similar motile stages can produce grossly different cysts and an extensive reclassification is likely to ensue when more work has been done on encystment. It is therefore unsatisfactory to press fossil cysts into a taxonomic system based largely on living motile stages as Eisenack has done, when we know so little about the life cycles and important reclassification of the living forms is impending.

The frequent dissimilarity between the motile and cyst stages means that attribution of a cyst to a species based on a motile stage can only be confidently asserted on the direct evidence of cultures or on the circumstantial evidence of close geographic association of certain cyst types with certain motile stage types. Neither of these possibilities is available to the palynologist who at the most can hope to identify a fossil cyst with a Recent one by morphological comparison. In an overwhelming number of instances he can expect to find no exact counterpart, and his classification must be a classification of cysts.

It is hoped to deal more thoroughly with the classification of fossil dinoflagellate cysts in a separate publication where the whole range of cyst types can be considered adequately.

III. STRATIGRAPHY AND HISTORICAL BACKGROUND

a. The Speeton Clay

By W. A. S. SARJEANT

The Speeton Clay is the lowest of the three horizons principally dealt with in this work. Two boreholes were put down through the Speeton Clay during the summer of 1960 by Koninklijke Shell Exploratie en Produktie Laboratorium, Rijswijk, The Netherlands. The first of these, Shell Speeton No. 1, was sited near Speeton Beck (grid ref. TA.151753) and reached a depth of 135.25 metres (443 ft. 11 in.) ; the second, Shell West Heselton No. 1, was put down at West Heselton, some 1.4 miles west of Speeton, reaching a depth of 117 metres (383 ft. 4 in.) without bottoming the Lower Cretaceous. Through the courtesy of Shell Internationale Research Maatschappij N.V., The Hague, Netherlands, specimens were made available for micropalaeontological and palynological study to various specialists. Results of study of the Speeton Clay ostracod faunas have been published by Neale (1960*a*, 1962*a*), Neale & Kilenyi (1961) and Kaye (1963*a*, 1963*b*, 1964*a*). These authors also published accounts of the outcrop stratigraphy (Neale 1960*b*, 1962*b* ; Kaye 1964*b*) ; their accounts of the stratigraphy and ostracod faunas of the boreholes are currently in press.

The assemblages of fossil microplankton proved unexpectedly rich. They are dominated by dinoflagellate cysts, acritarchs being relatively infrequent. Studies have to date been concentrated on the assemblages from the West Heselton borehole, a brief account of some new species from a Hauterivian horizon having already been published (Neale & Sarjeant 1962). The holotypes of the species described in that paper, formerly in the collections of the Sedimentology Research Laboratory, University of Reading, are now lodged in the British Museum (Natural History) under the following numbers :

Species	Reading Nos.	B.M.(N.H.)
<i>Heslertonia heslertonensis</i> (formerly <i>Gonyaulax</i>)	44Y/8/10	V.51713(1)
<i>Gonyaulacysta cretacea</i> (formerly <i>Gonyaulax</i>)	44Y/4/21	V.51711(2)
<i>Cribroperidinium sepimentum</i>	44Y/7/7	V.51712 (1)
<i>Gardodinium albertii</i>	44Y/1/28	V.51709(2)
<i>Pseudoceratium</i> (<i>Eopseudoceratium</i>) <i>gochti</i>	44Y/1/36	V.51709 (4)
<i>Muderongia crucis</i>	44Y/4/1	V.51711(1)
<i>Heliodinium patriciae</i>	44Y/3/3	V.51710(1)
<i>Oligosphaeridium vasiformum</i> (formerly <i>Hystrichosphaeridium</i>)		
Holotype	44Y/1/34	V.51709(3)
Paratype	44Y/1/26	V.51709(1)
<i>Oligosphaeridium macrotubulum</i> (formerly <i>Hystrichosphaeridium</i>)	44Y/7/20	V.51712(2)
<i>Systematophora complicata</i>	44Y/4/22	V.51711(3)

Subsequently, examination of assemblages has been extended upwards into the Barremian. In the chapters which follow, the results are given of studies by R. J. Davey and the writer on the dinoflagellate cysts from five assemblages in the West Heselton No. 1 Borehole, as follows :

Depth	Character of Sediment	Stage
19.25/50 metres	Soft, medium dark grey (N ₄) to live grey (SY _{4/1}) clay, containing much pyrite.	Upper Barremian (Middle part)
39.00/25 metres	Softish, medium (N ₅) to olive grey (5Y _{5/1}) clay, pyritic, with some shell fragments.	Middle Barremian (Cement Beds)
42.50/75 metres	Lithology as last.	Lower Barremian (top)
99.25/50 metres	Hard, medium olive grey (5Y _{5/1}) siltstone, laminated and pyritic.	Middle Hauterivian
103.25/50 metres	Well-laminated olive grey (5Y _{6/1}) pyritic clay, rather streaky, with shell fragments.	Middle Hauterivian

(The numbers in parentheses are the American Rock Colour Chart numbers.)
For further stratigraphical information, see forthcoming paper by Neale & Kaye.

b. The Lower Chalk

By R. J. DAVEY

Fossil microplankton from the Upper Chalk (Senonian) of Great Britain were first described in the mid-nineteenth century by a group of amateur microscopists, namely Mantell, Reade, Deane, White, Bowerbank and Wilkinson. After these initial studies no subsequent work was performed in Great Britain on Upper Cretaceous microplankton until 1964, when Cookson & Hughes published a paper on microplankton from the Cambridge Greensand, of presumed basal Cenomanian age. The work referred to in the following chapters, on microplankton assemblages from the English Lower Chalk (Cenomanian), is part of a larger study of the Cenomanian assemblages throughout the world.

Specimens quoted in this paper as being of Cenomanian age have all been obtained from samples from H.M. Geological Survey Borehole at Fetcham Mill, Leatherhead, Surrey (National Grid Reference, TQ.158565). At this locality the Cenomanian is 197 feet thick and lies conformably on the Upper Greensand. The basal Cenomanian is a grey, glauconitic impure chalk containing a relatively high percentage of clay minerals. The percentage of clay minerals progressively decreases towards the top of the stage where the Cenomanian is a hard, almost pure, white chalk. A full account of the stratigraphy appears in the Geological Survey Bulletin No. 23.

Ten samples, at twenty foot intervals, were analysed for their organic-shelled microplankton content. The microplankton content was quite rich and fairly well preserved. Cysts of dinoflagellates were predominant over acritarch remains, and spores and pollen were relatively rare.

c. The London Clay

By G. L. WILLIAMS & C. DOWNIE

Dinoflagellate cysts (hystrichospheres) were first briefly recorded from the London Clay by E. W. Wetherell (1892). No further work was done on them for over 60 years. They first came to the attention of one of us (C.D.) in 1958, when Murray Hughes of the Geological Survey sent for identification a number of species picked out from washed foraminifera preparations which had come from London Clay at Isleworth, Middlesex. Mr. D. Curry (1958 : 56) had however previously exhibited hystrichospheres from the Eocene at a meeting of the Geologists' Association in November 1957. Subsequently Eager & Sarjeant (1963) recorded *Hystrichosphaeridium* similarly obtained from Berkshire. Mackó (1963) figured a variety of forms from the London Clay without identifying any of them conclusively.

The first systematic work on the dinoflagellates of the formation was begun in 1960 in Sheffield by G. L. Williams. His thesis (1963) dealt with all the planktonic dinoflagellates and acritarchs in the samples examined. Many of these were derived from older formations and are being described elsewhere ; the indigenous acritarchs and dinoflagellates will be listed here, but the acritarchs will not be described. Dinoflagellates belonging to *Hystrichosphaera*, *Haplosphaeridium*, *Cleistosphaeridium*, *Hystrichosphaeridium* and allied genera are treated by Davey & Williams in Sections IV and V of the present work.

STRATIGRAPHY. The London Clay is confined to two areas in Southern England, the London and Hampshire Basins respectively. They formed one continuous basin of deposition during Eocene times but subsequent orogenic movements and erosion have given rise to the intervening Wealden Dome separating the two main outcrops of the London Clay. The term basin when speaking of the two areas is therefore used in a structural sense referring to the present day conditions only. There is close similarity between the lithology of the London Clay of the western margin of the London Basin and of the Hampshire Basin where the " typical " stiff blue grey clay is increasingly replaced by arenaceous beds, loamy and sandy bands being common.

To the east of the London Basin, the blue clay reaches its greatest thickness, at Sheppey, where it is estimated to be over 500 feet thick with little change in lithology throughout. Collecting was undertaken at three places, Studland Bay in Dorset, Whitecliff Bay in the Isle of Wight, both in the Hampshire Basin, and Sheppey in the London Basin. In addition, Professor H. L. Hawkins kindly provided samples from borehole cores from the Enborne Valley, lying in the west of the London Basin where the lithology shows striking similarities to that of the Hampshire Basin.

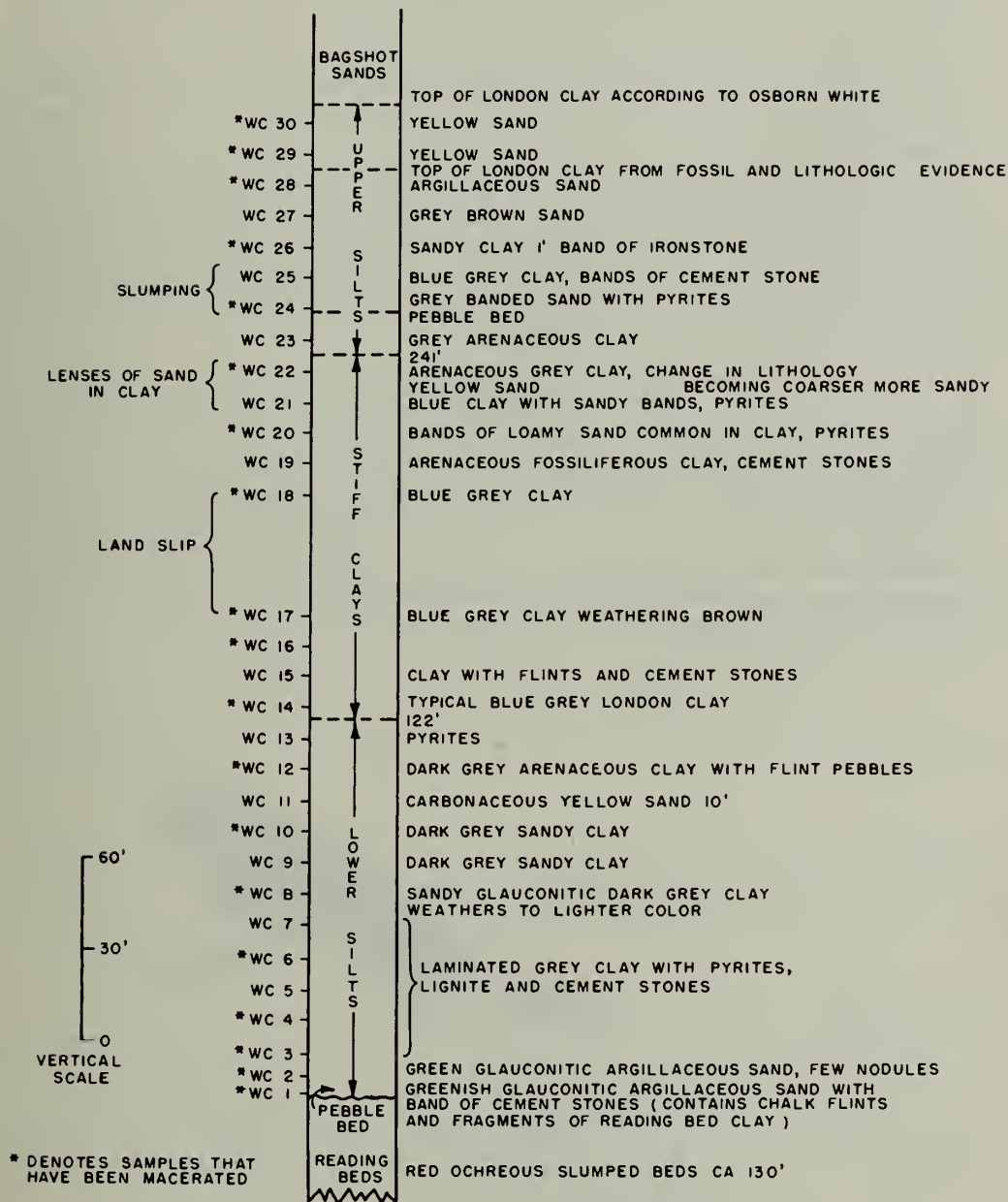


FIG. 5. Succession of the London Clay at Whitecliff Bay, showing the location of samples.

STUDLAND BAY. One of the most westerly outcrops of the London Clay is found at Studland Bay in Dorset, where conditions in the Lower Eocene fluctuated between marine and fresh-water, being very close to, and at times marking, the shoreline of the London Clay sea. As with all cliff sections of the London Clay, difficulty is experienced in collecting because of slumping. This obscures most of the London Clay but fortunately both lower and upper junctions with the Reading and Bagshot Beds are exposed.

Because of the poor exposures, samples could only be taken haphazardly, three (ST. 1-3) being collected within 10 feet of the base, and one (ST. 4) from only three feet below the junction with the Bagshot Beds. The London Clay at Studland is, at the base, an arenaceous yellow brown clay passing upwards into a friable yellow argillaceous sand; the succeeding Bagshot Beds are almost pure quartz sands, bright yellow in colour and partly consolidated.

ISLE OF WIGHT. The exposures of London Clay in the Isle of Wight at Alum Bay and Whitecliff Bay are of importance because they give the only continuous exposures through the whole London Clay, from the junction with the Reading Beds to the base of the Bagshot Sands. The dip of the beds is almost vertical and they strike at right angles to the exposure, thus providing comparatively easy conditions for collecting. The main difficulty is slumping or slipping, which is a common occurrence in the Alum Bay section, less frequent at Whitecliff. Only the Whitecliff section has been studied because it is less affected by slumping and the junction of the London Clay and Bagshot Beds can be more precisely placed.



FIG. 6. Map of South-east England, showing in black the outcrop of the London Clay. The localities from which samples were collected are shown by the arrows.

According to the earliest authority on the Eocene of Whitecliff, Prestwich (1847), the thickness of his beds 3 and 4, (which he called the Bognor Beds), is 307 feet. These are equivalent to the London Clay. Bristow (1862) lists a succession but attempts no estimation of thickness. In the revised Isle of Wight Memoir of 1889, the section is not given in detail, but an approximate value of 320 feet for the thickness of the London Clay is quoted by Reid. The pebble bed according to Reid is 255 feet above the base. The first detailed section is attributable to White (1921) who measured a total of 322 feet, with the pebble bed at 285 feet above the base. Since 1921 all authorities including Curry (1958a) have quoted this thickness of 322 feet for the London Clay of Whitecliff. In measurements carried out by the authors with a tape measure a value of 300 feet was arrived at for the thickness of the London Clay with the pebble bed at 255 feet. Samples were taken for 315 feet above the base but the two topmost (305, 315 feet) were yellow sands barren of microplankton.

Lithologically, the London Clay at Whitecliff is roughly divisible into three units equivalent to the Lower Silts, the Stiff Clays and the Upper Silts of the Enborne Valley (Hawkins 1954). Within each of these three units alternations of clays and sands with all degrees of intermingling often occur and septarian nodules, lignite and iron pyrites are common throughout. Sample numbers are shown in Text-fig. 5.

ENBORNE VALLEY (Berkshire). In the years 1947-49 a series of borings were sunk in the eastern part of the Enborne Valley, penetrating beds primarily of Eocene age, much of which was London Clay. Professor H. L. Hawkins has kindly allowed us to take samples from cores in his possession. Two boreholes, numbers 11 and 39 whose geographical positions can be seen in Text-fig. 6, were examined.

According to Hawkins (1954), the London Clay of the Enborne Valley is lithologically divisible into three sections, the Lower Silts, the Stiff Clays and the Upper Silts.

From boring number 11, six samples have been examined in detail, one from the Upper Silts, four from the Stiff Clays and one from the Lower Silts. From boring number 39, four samples have been studied, three from the Stiff Clays, one from the Lower Silts. All the samples studied yielded microplankton usually in a good state of preservation (see Text-fig. 7).

SHEPPEY. The London Clay attains its maximum thickness at Sheppey where Davis (1936) has estimated it to be 518 feet. Of this the upper 160 feet are exposed in the Sheppey cliff section running for six miles in an east-south-east direction from Scrapgate in the west to Warden Point in the east. The lithology is a uniform stiff blue grey clay with frequent courses of septaria. The junction with the Bagshot Beds is well exposed in the west where 10 feet of *in situ* Bagshot sand overlies the London Clay; elsewhere difficulty is caused by large scale slipping and the number of samples collected is less than might have been desired.

Wrigley (1924) proposed five divisions for the London Clay of the London Basin, each characterized by a faunal suite but not zones in the strictest sense. The fifth (uppermost) division is typically sandy with more frequent fossils than blue clay.

	STUDLAND				WHITECLIFF				ENBORNE 11				ENBORNE 39	SHEPPEY			
<i>Achomosphæra alicornu</i> (Eis.) <i>ramulifera</i> (Defl.) <i>ramulifera</i> v. <i>perforata</i> nov.	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
<i>Cannosphaeropsis reticulensis</i> Pastiels <i>Nematosphaeropsis balcombiana</i> Defl. & Cooks.	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
<i>Cyclonephaleum pastiedsi</i> Defl. & Cooks. <i>exuberans</i> Defl. & Cooks. <i>ordinatum</i> sp. nov. <i>divaricum</i> sp. nov.	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
<i>Areoligera coronata</i> (O. Wetz.) cf. <i>coronata</i> (O. Wetz.) cf. <i>madusettiformis</i> (O. Wetz.) cf. <i>senonensis</i> Lej. Carp.	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
<i>Wetzeliella articulata</i> Eis. v. <i>conopia</i> nov. <i>coleothrypra</i> sp. nov. <i>reticulata</i> sp. nov. <i>tenuiturgula</i> sp. nov.	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
<i>tenuiturgula</i> v. <i>crassoramosa</i> nov. <i>homomorphia</i> Defl. & Cooks. <i>homomorphia</i> v. <i>quinquelata</i> nov.	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
<i>ovalis</i> Eis. <i>condylos</i> sp. nov. <i>similis</i> Eis. <i>symmetrica</i> Weiler <i>symmetrica</i> v. <i>lobisca</i> nov. <i>variolongituda</i> sp. nov. <i>glabra</i> Cooks.	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
<i>Deflandrea phosphoritica</i> Eis. <i>phosphoritica</i> v. <i>australis</i> Cooks. Eis. <i>wardensis</i> sp. nov. <i>wardensis</i> v. <i>quinquelata</i> nov. <i>oebisfeldensis</i> Alberti	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
<i>Thalassiphora pelagica</i> Eis. & Gocht <i>delicata</i> sp. nov.	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x

The occurrence of indigenous species of Dinoflagellate cysts in the London Clay

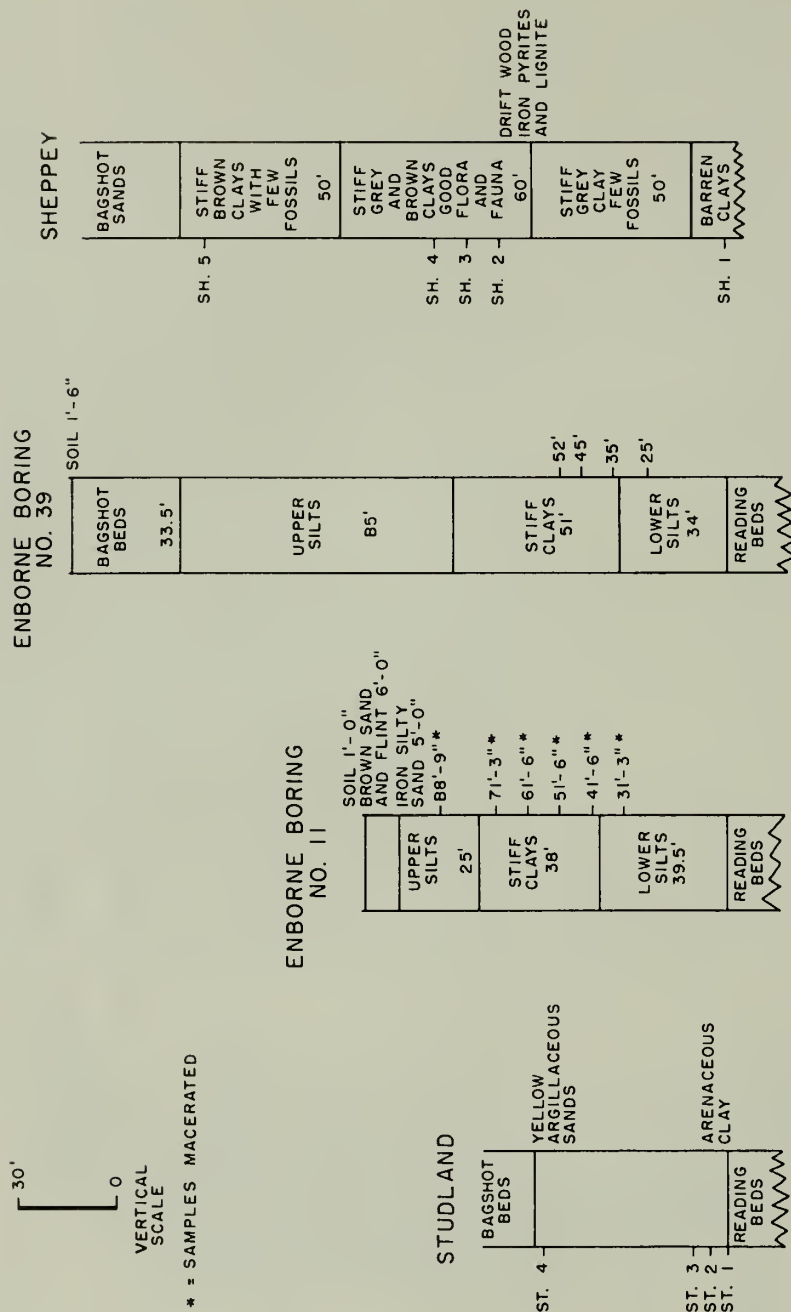


Fig. 7. The successions of the London Clay at Studland, Enborne and Sheppey showing the location of samples.

This uppermost division is represented at Sheppey by a continuation of the fourth division whose stiff clays with septaria come in 300–350 feet above the base. It is probable that most of the London Clay exposed at Sheppey falls within this (the fourth) division, the only possible exception being the “Foreshore Beds” of Davis (1936) which may mark the top of the third division. The first, second and most of the third divisions of Wrigley (1924) lying below the surface at Sheppey, only outcrop further east at Herne Bay and Reculver Bay, and are at present being investigated by Mr. A. Hussain in the Department of Geology at Sheffield University.

Davis recognized the following sequences in the Sheppey cliff section :

- | | |
|--|-----|
| (d) Stiff brown clays with few fossils | 50' |
| (c) Stiff grey and brown clays with good fauna and flora in
lower part. Rarely <i>in situ</i> | 60' |
| (b) Stiff blue clays. Few fossils. | 50' |
| (a) Foreshore. Barren clays, blue or lead coloured. | — |

Group (a) The “Foreshore Beds”, probably include the upper parts of Wrigley’s third division, whilst beds (b), (c) and (d) seem to belong to his fourth division, (d) including the Sheppey equivalent of Wrigley’s division five. Samples have only been collected from groups (a), (c) and (d) because group (b) was never clearly exposed (Text-fig. 7).

IV. THE GENERA *HYSTRICHOSPHAERA* AND *ACHOMOSPHAERA*

By R. J. DAVEY & G. L. WILLIAMS

INTRODUCTION

The celebrated German microscopist, C. G. Ehrenberg, was the first to notice the occurrence of minute spiny organisms in flakes of Upper Cretaceous flint. These organisms were divided by him into two types. The first type possessed oval to polygonal shells bearing numerous forked processes and characterized by two furrows, one encircling the shell and the other perpendicular to it on one surface only. Such forms he recognized as belonging to a group of present-day plankton, the dinoflagellates. The second type had spherical or oval shells bearing forked processes as before but not possessing furrows. These forms he found rather difficult to identify, but came to the conclusion that they were silicified zygospores of a freshwater desmid known as *Xanthidium*. His initial findings were published in 1838 and 1843.

In 1838 Ehrenberg came to England and visited the Clapham Microscopical Society where he greatly influenced a group of British microscopists—Mantell, Reade, Deane, White and Wilkinson. Mantell (1845), after critically examining the shells of the *Xanthidia*, came to the conclusion that they were composed of some flexible substance, probably organic, perhaps chitin or cutin. Later (1850) he suggested that the spiny spheres were "probably the gemmules of sponges or other zoophytes", and proposed the new genus *Spiniferites* to include them. This new name, however, was overlooked by subsequent workers and was eventually abandoned as a *nomen nudum* (Sarjeant 1964).

In 1904 the German marine biologist, Lohmann, after having worked on modern plankton and examined the fossil spiny spheres, decided that the latter were definitely planktonic. He came to the conclusion that they were eggs of a marine crustacean, probably a Copepod, and for this reason gave them the name *Ova hispida*. Reinsch (1905), for the first time, considered these fossils to be the cysts of marine algae, possibly dinoflagellates. He termed them "palinospheres", another name which never came into general use.

O. Wetzel (1933) rejected all previous attributions and placed them in a new family, Hystrichosphaeridae, of unspecified systematic position. All the described species were included in his new genus *Hystrichosphaera*, and *Hystrichosphaera furcata* and *H. ramosa* were designated as joint type species.

Deflandre (1937) emended Wetzel's genus *Hystrichosphaera* to include only those forms possessing an equatorial girdle and polygonal fields. His choice of *H. furcata* as the sole type species has, however, proved an unfortunate one. Those forms without surface ornamentation he placed in a new genus, *Hystrichosphaeridium* Deflandre.

Evitt (1961) considered that *Hystrichosphaera* was not a motile dinoflagellate but a cyst possessing structures which are reflections of features seen in the motile stage. The presence of a precingular archaeopyle was noted and compared with that present

in *Gonyaulacysta* (Deflandre 1964). In 1963 he erected the genus *Achmosphaera* to accommodate species possessing a precingular archaeopyle and processes of the same form and distribution as found in the genus *Hystrichosphaera*, but lacking sutural crests or membranes.

Genus *HYSTRICHOSPHAERA* O. Wetzel 1933 : 33

1937. *Hystrichosphaera* O. Wetzel ; Deflandre : 61.

EMENDED DIAGNOSIS. Chorate to proximo-chorate cysts possessing a sub-spherical or ovoidal central body with a clearly defined reflected tabulation of 3-4', 6'', 6c, 5''', 0-1p, 1''''', plate 6'' being generally reduced and triangular. Wall of central body composed of two layers, an inner endophragm and an outer periphragm. Cingulum always disposed in a laevo-rotatory spiral. Plate boundaries indicated by variably developed sutural crests or membranes, and gonial and sutural processes. Processes open or closed, solid or hollow, simple or branching. Length of processes variable, sometimes not extending beyond sutural crests, apical pole often marked by an elongate process. Archaeopyle precingular, formed by loss of reflected plate 3''.

TYPE SPECIES. *Xanthidium ramosa* Ehrenberg 1838. Upper Cretaceous (Senonian) ; Germany.

REMARKS. The generic diagnosis is emended to include reference to the reflected tabulation and to the presence of sutural processes in many species attributable to this genus.

The *Hystrichosphaera furcata-ramosa* complex

It is difficult to distinguish between *H. furcata* (Ehrenberg) and *H. ramosa* (Ehrenberg). The original drawings of Ehrenberg are inadequate for the present refined morphological studies and there is no description accompanying the figures of the types. The types for both species have either been lost or have not been re-examined recently, and many varied interpretations of the species have been made by later workers.

Ehrenberg (1838) figured a number of specimens as *Xanthidium furcatum* and *Xanthidium ramosum* without description or holotypes. His figures show that the main difference between the two species is the form of the extremities of the processes. *X. furcatum* has predominantly bifurcate processes ; only one of the figures (pl. 1, fig. 14a) shows trifurcate processes and then these do not predominate. *X. ramosum* has predominantly trifurcate processes and branching is shown to occur occasionally from a medial position on the processes. Branching is absent from Ehrenberg's figures of *X. furcatum*. The names given to the species confirm that Ehrenberg distinguished them on the type of process present.

White (1842) published the first account of both species. *X. furcatum* he described as having numerous, regularly arranged processes which gradually taper distally ;

thus they are not furcate. His figures are certainly not in accordance with those of Ehrenberg, and probably represent a different species. White's figures of *X. ramosum* closely resemble those of Ehrenberg for this species and are probably correct. The processes are predominantly trifurcate, often with a small bifurcation at their extremities.

X. ramosum had been figured earlier, without description, by Reade (1839) but his figure more closely resembles *X. complex* White than Ehrenberg's figures of *X. ramosum*. Ehrenberg (1854) refigured some of his specimens but again they were not accompanied by a text description.

O. Wetzel (1933) erected the genus *Hystrichosphaera* making both *H. furcata* and *H. ramosa* type species, this being contradictory to the rules of nomenclature. *H. furcata* is described as having strongly built processes with short bifurcations distally, each branch terminating in two spines. In *H. ramosa* some of the processes are divided into two, rarely more, they branch approximately half way along their length and finally divide into spinelets, usually three in number. The descriptions correspond with Ehrenberg's specimens, but O. Wetzel's plates are not distinct. Both species possess central bodies which are divided into fields or areas by sutures, from the junctions of which 6 to 30 processes arise. An equatorial girdle is often present. O. Wetzel considered *H. furcata* and *H. ramosa* to be varieties of the same species, and contrary to the rules of nomenclature, proposed a new name *H. communis* to contain them.

Deflandre (1935, 1936) figured a specimen of *H. furcata* which differs from Ehrenberg's types in that there is a proximal membrane and the majority of the processes have trifurcate extremities. Later (1937) he published the first account of the tabulation of *H. furcata* and also mentioned the well developed apical process. He pointed out that the processes invariably arose from nodal points at the junction of the plates. The processes are short and predominantly trifurcate, although some bifurcate processes do occasionally occur. The number of processes is approximately 30. The processes are not of equal length and tend to be shortest in the region of the triangular plate and longest at the poles. *H. ramosa* as figured by Deflandre differs from *H. furcata* only in the presence of processes which divide medially into two branches which themselves terminate distally in three spines. Like Wetzel Deflandre also considered *H. furcata* and *H. ramosa* to be varieties of one species, but suggested that the names *H. furcata* and *H. furcata* var. *ramosa* would be more appropriate, the latter being applied to individuals having slender and very divided processes. However the plates show only slight differences between the two types. Both possess bifurcate and trifurcate processes with medial branching and proximal membranes; and considering the slenderness of the processes there is little or no difference. In fact both forms agree very well with *X. ramosum* of Ehrenberg.

Lejeune (1937) re-examined Ehrenberg's preparations and rediscovered one of his figured specimens (pl. 1, fig. 1) of *X. ramosum*. A detailed description of *H. ramosa* was given by Lejeune accompanied by some excellent figures. The majority of the

processes are trifurcate but some of the processes occupying a medial position are shown to be bifurcate. Some of the trifurcate processes possess small terminal bifurcations, and the membranes are always shown to be proximal. The number of processes is said to be approximately 40. Unfortunately, *H. furcata* was not similarly treated, Lejeune having apparently failed to recognize any of the original specimens figured by Ehrenberg as *Xanthidium furcatum* Ehrenberg.

Valensi (1955) described forms in which the processes terminate in two small spines or a fork. However his figures do not always correspond to the description given. Some of the processes are open with serrate lips and others are trifurcate with distal bifurcations. Some of the specimens have prominent crests with elevated membranes and differ from both of Ehrenberg's forms.

Eisenack (1958) described specimens attributed to *H. furcata* from the Aptian of Germany having short, thick processes with broad bases and dividing into two or three spines distally. In his description he emphasized the wide degree of variation in the species as interpreted by earlier workers.

Maier (1959) described and figured *H. furcata* from the Miocene of Germany, her forms possessing solid processes which divide distally in two to four spines. Gocht (1959) described specimens of *H. furcata* from the Neocomian of Germany as sometimes having isolated processes while others possessed well developed membranes along the plate boundaries uniting adjacent processes. *H. ramosa*, as described by Gerlach (1961), from the German Oligocene, possesses oval central bodies and trifurcate processes which are bifurcate distally.

Brosius (1963) restricted *H. furcata* to forms with bifurcate and trifurcate processes and *H. ramosa* to those with trifurcate processes, each furcation terminating in a short bifurcation. Cookson & Hughes (1964) had difficulty in identifying *H. ramosa* in the Albian/Cenomanian of Cambridge and distinguished it from *H. furcata* by its larger size, thicker-walled processes, more strongly outlined fields and more pronounced membranes.

Since the two species were first figured by Ehrenberg, there has been considerable difference of opinion as to how each species should be diagnosed, and subsequent authors appear to have attributed their specimens somewhat randomly to one, or more rarely, to both species. As Lejeune (1937) first pointed out with reference to these species in the Upper Cretaceous they, and closely related forms, form a continuous varying complex. One can treat such a complex in one of two ways. All described forms can be grouped under one species heading and varieties created or the group may be further subdivided, each new species being clearly defined. Detailed study of the Cenomanian and London Clay forms included within this complex rules out the adoption of the second alternative, since variation is so great as to render the interpretation of separate species, that would be of practical value, difficult if not impossible.

One of the specimens designated as *Xanthidium ramosum* by Ehrenberg (1838, pl. 1, fig. 15) was located by Lejeune (1937). This specimen (refigured in pl. 1, fig. 1) and another of Ehrenberg's preparations have been fully studied by one of the

authors (R.J.D.). The preparations, which are now in the Humboldt University, Berlin, were kindly lent for examination by Dr. K. Diebel whose assistance is gratefully acknowledged.

Specimens of *X. furcatum* as illustrated by Ehrenberg (1838, pl. 1, figs. 12, 14) cannot be traced and are either not distinctive enough for sure identification with his drawings or they have subsequently been lost. It is therefore proposed to treat the complex as one species to be designated *Hystrichosphaera ramosa*, since none of the specimens of *X. furcatum* as figured by Ehrenberg has been positively identified by later workers. The specimen figured by Ehrenberg (1838, pl. 1, fig. 15) is erected as the holotype of *H. ramosa* and the species is regarded here as the type species of the genus. Since Ehrenberg did not designate a holotype or give a description of *H. furcata*, and since later workers have failed to recognize it, it is proposed that forms attributed to *H. furcata* since 1933 be transferred to *H. ramosa* Ehrenberg.

Hystrichosphaera ramosa, in its revised acceptation, is an extremely long ranging species exhibiting a very considerable degree of variation in the detail of its morphology. Many of the extreme variants, encountered in isolation, would be considered sufficiently morphologically distinct from the typical forms to justify their erection as separate species; but consideration of the whole assemblage shows all intermediate stages to be represented. However, our present knowledge of the species suggests that particular variational trends may have occurred only at certain stages within the total range of the species; the extreme variants are capable of ready recognition and may prove of value as stratigraphical indices. A number of varieties are therefore here proposed, distinguished on the bases of process number and form, combined with character of the periphragm. Each represents the extreme development of a particular structure or combination of structures; intermediate stages to the typical *H. ramosa* var. *ramosa* are in all cases known and are even frequent, so that differentiation of these forms at a higher taxonomic level is considered inappropriate.

***Hystrichosphaera ramosa* (Ehrenberg)**

EMENDED DIAGNOSIS. A species of *Hystrichosphaera* possessing a thin walled central body, smooth, reticulate or granular. Gonial $\pm$ sutural processes always extending beyond confines of sutural crests, solid or hollow, the latter closed distally. Typical gonial processes trifurcate, sutural processes bifurcate, both commonly terminating distally in a small bifurcation.

HOLOTYPE. Slide "Feuerstein von Delitzsch, no. XXV" of Ehrenberg, Institut für Paläontologie und Museum der Humboldt Universität, Berlin. Upper Cretaceous; Germany.

STRATIGRAPHICAL RANGE. This species has been recorded as *H. furcata* from the Oxfordian by Deflandre (1938) and Sarjeant (1960). Pleistocene examples have been observed by a number of workers, e.g. Fries (1951) and Rossignol (1964), and it has also been recorded from post-Pleistocene sediments dated 950 B.C. from West Wales. (Churchill & Sarjeant, in progress.)

***Hystrichosphaera ramosa* (Ehrenberg) var. *ramosa* nov.**

Pl. 1, figs. 1, 6 ; Pl. 3, fig. 1; Text-fig. 8

1838. *Xanthidium ramosum* Ehrenberg, pl. 1, figs. 1, 2, 5.
 1838. *Xanthidium furcatum* Ehrenberg, pl. 1, figs. 12, 14.
 1854. *Xanthidium ramosum* Ehrenberg, pl. 7, figs. 9, 10.
 1854. *Xanthidium furcatum* Ehrenberg, pl. 7, fig. 7.
 1932. *Hystrichosphaera furcata* (Ehrenberg) O. Wetzel : 136.
 1932. *Hystrichosphaera ramosa* (Ehrenberg) O. Wetzel : 144.
 1935. *Hystrichosphaera furcata* (Ehr.) ; Deflandre : 14, pl. 5, fig. 9 ; pl. 8, fig. 3.
 1936. *Hystrichosphaera furcata* (Ehr.) ; Deflandre : 62, text-fig. 108.
 1937. *Hystrichosphaera furcata* (Ehr.) ; Deflandre : 61, pl. 11, figs. 1-3.
 1937. *Hystrichosphaera ramosa* (Ehr.) ; Deflandre : 64, pl. 11, figs. 5, 7.
 1937. *Hystrichosphaera ramosa* (Ehr.) ; Lejeune : 239, pl. 1, figs. 2-4 ; pl. 2, figs. 5-10.
 1941. *Hystrichosphaera furcata* (Ehr.) ; Conrad, text-fig. 2, no. 1.
 1947. *Hystrichosphaera furcata* (Ehr.) ; Deflandre : 22, text-fig. 1, no. 11.
 1947. *Hystrichosphaera ramosa* (Ehr.) ; Deflandre : 22, text-fig. 1, no. 13.
 1952. *Hystrichosphaera furcata* (Ehr.) ; Deflandre, text-fig. 15.
 1952. *Hystrichosphaera ramosa* (Ehr.) ; Deflandre, text-fig. 17.
 1964. *Hystrichosphaera furcata* (Ehr.) ; Cookson & Hughes : 45, pl. 9, figs. 1, 2.

DIAGNOSIS. A variety of *H. ramosa* possessing an ovoidal central body bearing gonal and occasionally a small number of sutural processes. Gonal processes triangular in cross-section, sutural processes taeniate. Distally the processes are trifurcate or bifurcate often with bifid terminations, tapering to sub-conical in shape and sometimes branched. Sutural crests between processes proximal. Tabulation typical for genus.

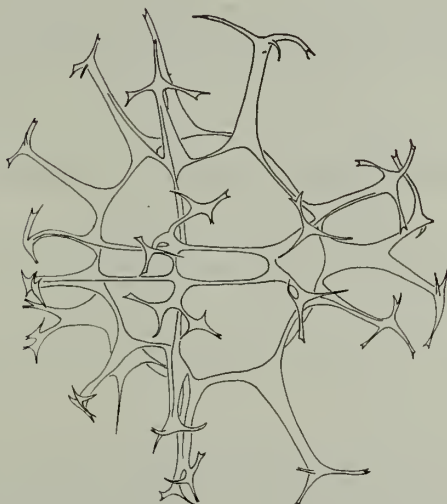


FIG. 8. *Hystrichosphaera ramosa* var. *ramosa* (Ehrenberg). The holotype, in lateral view. $\times$ c.700.

HOLOTYPE. Slide "Feuerstein von Delitzsch, no. XXV" of Ehrenberg (ringed in white on the third slice of flint). Lodged at the Institut für Paläontologie und Museum der Humboldt-Universität, Berlin. Upper Cretaceous; Germany.

DIMENSIONS. Holotype: diameter of central body 42 by 48 μ , length of processes 13–25 μ . Range of Lower Cretaceous (Barremian) specimens: diameter of central body 34–41 μ , length of processes 5–13 μ . Number of specimens measured, 2. Range of Cenomanian specimens; diameter of central body 30–50 μ , length of processes 7–27 μ . Number of specimens measured, 13. Range of London Clay (Ypresian) specimens; diameter of central body 32–56 μ , length of processes 11–20 μ . Number of specimens measured, 9.

DESCRIPTION. The plates of the cingulum are distinctive, being elongate and six-sided. There are two gonal processes between adjacent cingular plates and these are usually connected by a well developed membrane. The longitudinal furrow is obvious and is considerably larger on the hypotract. A distinctive simple apical process is commonly present. When the trapezoid precingular archaeopyle is present it is noticeable that the margin appears to lie just within the boundary of plate 3". One specimen of *H. ramosa* var. *ramosa* (Pl. 3, fig. 1) has been observed in the Upper Oxfordian (Throstler Clay, Upper Calcareous Grit) of England (Sarjeant 1960). The specimen is large (central body diameter 58 by 61 μ , length of processes up to 19 μ) but otherwise appears to be typical of this variety.

This variety has a known stratigraphic range from the Middle Barremian to the Ypresian.

REMARKS. *H. ramosa* var. *ramosa* is characterized by the form of its processes and the absence or scarcity of sutural processes. Doubtful descriptions or illustrations of forms classified as *H. furcata* or *H. ramosa* have not been included in the synonymy of *H. ramosa* var. *ramosa* and are placed in *H. ramosa* (Ehrenberg) var. indet. The varieties of *H. furcata* described by Rossignol (1964) must be transferred to *H. ramosa*.

***Hystrichosphaera ramosa* var. *gracilis* nov.**

Pl. 1, fig. 5; Pl. 5, fig. 6

1955. *Hystrichosphaera ramosa* (Ehr.) ; Deflandre & Cookson : 263, pl. 5, fig. 8.

1963. *Hystrichosphaera ramosa* (Ehr.) ; Górka : 48, pl. 6, figs. 6, 7.

DERIVATION OF NAME. Latin, *gracilis*, slender or graceful—with reference to the slender, rather delicate processes.

DIAGNOSIS. A variety of *H. ramosa* (Ehrenberg) with smooth, thin-walled central body bearing gonal and sutural processes. Processes solid or hollow and relatively long and slender. Crests proximal and extending along all processes often as far as the trifurcation. Gonal processes mainly trifurcate, sutural processes bifurcate, all but smallest terminating with small trifurcation.

HOLOTYPE. B.M.(N.H.) slide V.51757(1). 5 feet above the base of London Clay ; Sheppey, Kent.

DIMENSIONS. Holotype : diameter of central body 35 by 43 μ , length of processes 17–23 μ . Range of London Clay specimens ; diameter of central body 32–61.5 μ , length of processes up to 29 μ . Number of specimens measured, 7. Range of Cenomanian specimens ; diameter of central body 28–33 μ , length of processes up to 20 μ . Number of specimens measured, 3.

REMARKS. *H. ramosa* var. *gracilis* is characterized by the slender, relatively long, gonol and sutural processes. The position of the sutural processes in the examples studied appears to be haphazard.

The known stratigraphic range of this variety is from the Cenomanian (England) to the Miocene (Australia).

***Hystriosphæra ramosa* var. *granosa* nov.**

Pl. 4, fig. 9

DERIVATION OF NAME. Latin, *granosus*, granular—with reference to the granular nature of the surface of the central body.

DIAGNOSIS. A variety of *H. ramosa* (Ehrenberg) similar to *H. ramosa* var. *gracilis* except that the surface of the central body is coarsely granular. Height of granules ranging up to 0.5 μ .

HOLOTYPE. B.M.(N.H.) slide V.51752(2). 78 feet above the base of London Clay ; Sheppey, Kent.

DIMENSIONS. Holotype : diameter of central body 35 by 42 μ , length of processes up to 19 μ . Range : diameter of central body 33–45 μ , length of processes up to 19 μ . Number of specimens measured, 4.

REMARKS. A small number of specimens have been observed in the London Clay that apparently do not possess sutural processes. However, there is a complete gradation from these forms to those bearing many sutural processes and so separation solely on this characteristic was not thought to be practical.

H. ramosa var. *granosa* has only been recorded from the London Clay of England.

***Hystriosphæra ramosa* var. *multibrevis* nov.**

Pl. 1, fig. 4 ; Pl. 4, fig. 6 ; Text-fig. 9

1955. *Hystriosphæra furcata* (Ehr.) ; Valensi : 586, pl. 4, fig. 4 ; pl. 5, fig. 12.

1958. *Hystriosphæra furcata* (Ehr.) ; Eisenack : 406, pl. 25, figs. 4–8.

DERIVATION OF NAME. Latin, *multus*, much ; *brevis*, short—with reference to the large number of short processes present in this variety.

DIAGNOSIS. A variety of *H. ramosa* (Ehrenberg) with smooth or slightly reticulate central body bearing short solid processes less than half the diameter of central body in length. Gonol processes trifurcate, sutural usually bifurcate, both types usually

terminating with a small bifurcation. Number and size of sutural processes varying considerably, up to three between adjacent gonial processes. Sutural crests proximal or well developed and always extending along gonial processes, making the latter subconical in shape. When the crests are well developed, the sutural processes may be reduced to delicate protuberances emanating from the crest border.

HOLOTYPE. B.M.(N.H.) slide V.51981(1). Metropolitan Water Board Borehole No. 11 at 63 feet depth, London Clay; Enborne, Berkshire.

DIMENSIONS. Holotype: diameter of central body 35 by 44.5μ , length of processes up to 14μ . Range of London Clay specimens; diameter of central body $35-59\mu$, length of processes up to 16μ . Number of specimens measured, 6. Range of Hauterivian and Barremian specimens; diameter of central body $34-47\mu$. Length of processes up to 12μ . Number of specimens measured, 7. Range of Cenomanian specimens; diameter of central body $31-46\mu$, length of processes up to 19μ . Number of specimens measured, 11.

REMARKS. *H. ramosa* var. *multibrevis* is characterized by the presence of short gonial and sutural processes. Examples from the Lower Cretaceous possess very short, rather rudimentary processes and differ from *H. dentata* (Gocht 1959) in having the characteristic tabulation of the genus which is lacking in Gocht's species. In the Cenomanian the processes are better developed but rather variable in form,

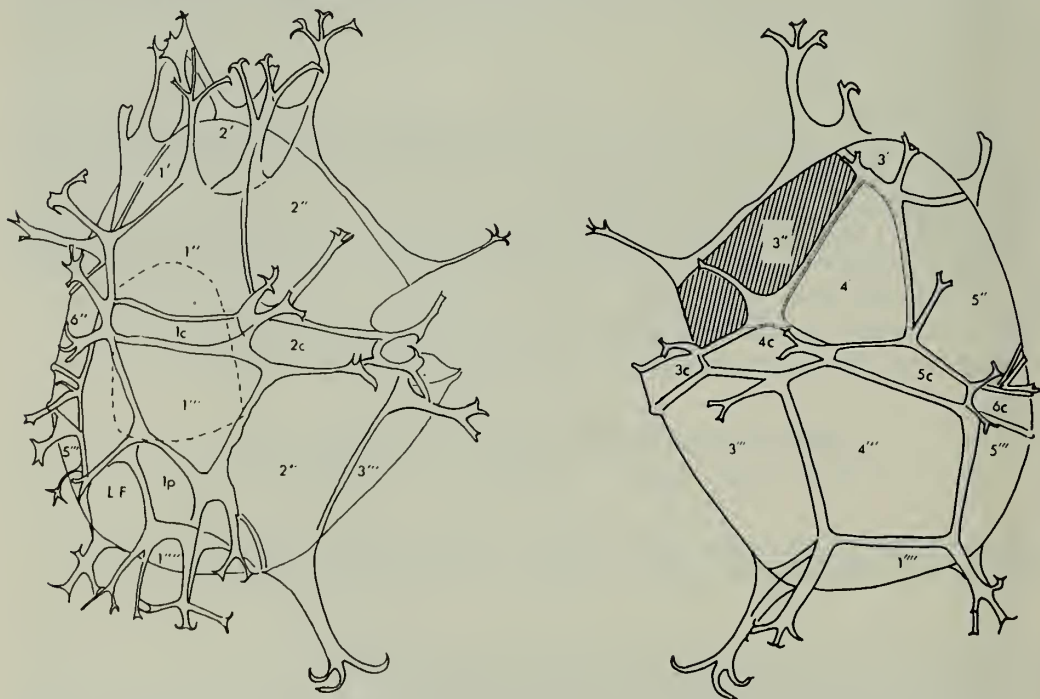


FIG. 9. *Hystrichosphaera ramosa* var. *multibrevis* nov. A specimen from the London Clay. Left, ventral view. Plate 3'' (the operculum of the archaeopyle) lies within the central body. Right, dorsal view. $\times$ c.1500.

stability being reached in the Eocene when the processes resemble those found in *H. ramosa* var. *ramosa* but are shorter and subconical, and considerably more numerous. *H. ramosa* var. *multibrevis* is similar to *H. furcata* var. *multiplicata* (Rossignol 1964) from the Pleistocene of the Eastern Mediterranean except for the absence of the two distinctive large dorsal antapical processes.

H. ramosa var. *multibrevis* has been recorded from the Lower Cretaceous (Hauterivian) to the Eocene (Ypresian) in England, from the Upper Cretaceous of France and from the Aptian of Germany.

***Hystrichosphaera ramosa* var. *membranacea* (Rossignol)**

Pl. 4, figs. 8, 12

1964. *Hystrichosphaera furcata* var. *membranacea* Rossignol : 86, pl. 1, figs. 4, 9, 10 ; pl. 3, figs. 7, 12.

MATERIAL (Figured). B.M.(N.H.) slide V.51747(2). Metropolitan Water Board Borehole No. 11 at 53 feet depth, London Clay ; Enborne, Berkshire. Micropal. Lab., Sheffield University No. SL5. 173 ft. above base of London Clay ; Sheppey, Kent.

DIMENSIONS. V.51747(2) : diameter of central body 38.5 by 43 μ , length of processes up to 19 μ . Observed range : diameter of central body 31.5–45 μ , length of processes up to 26 μ . Number of specimens measured, 5.

REMARKS. The specimens belonging to this variety found in the London Clay agree fairly well with those observed by Rossignol (1964) from the Pleistocene. *H. ramosa* var. *membranacea* possesses a smooth walled central body with well developed membranes on the plate boundaries. The membranes are variable in height and development and may unite all or only few of the processes. However the membranes are commonly well developed only in the cingular and polar regions. The two large dorsal antapical processes noted by Rossignol are not noticeable in the Eocene forms.

The often extensive development of a membrane in the equatorial zone restricted to one side gives some of the specimens a superficial resemblance to the form figured as *H. ramosa* by Lejeune (1937).

***Hystrichosphaera ramosa* var. *granomembranacea* nov.**

Pl. 4, fig. 4

DERIVATION OF NAME. Latin, *granosus*, granular ; *membrana*, membrane— with reference to the granular membranes present in this variety.

DIAGNOSIS. A variety of *H. ramosa* (Ehrenberg) possessing a central body with a granular surface. Membranes well developed on plate boundaries particularly in cingular and polar regions.

HOLOTYPE. B.M.(N.H.) slide V.51982(1). 99 feet above base of London Clay ; Sheppey, Kent.

DIMENSIONS. Holotype : diameter of central body 47 by 49 μ , length of processes up to 20 μ . Range : diameter of central body 41.5–56 μ , length of processes up to 27 μ .

REMARKS. This variety is similar to *H. ramosa* var. *membranacea* except that the surface of the central body is granular ; it has only been recorded from the London Clay of England.

***Hystrichosphaera ramosa* var. *reticulata* nov.**

Pl. I, figs. 2, 3

DERIVATION OF NAME. Latin, *reticulatus*, net-like—with reference to the reticulate nature of the periphragm.

DIAGNOSIS. A variety of *H. ramosa* (Ehrenberg) with central body composed of thin smooth endophragm and reticulate periphragm. Gonial and occasionally sutural processes triangular, taeniate or subconical. Gonial processes trifurcate and suturals bifurcate, both types usually terminating distally with small bifurcation. Crests commonly reticulate, proximal except where they extend along processes.

HOLOTYPE. Geol. Surv. Colln., slide PF.3038(1). Lower Chalk, H.M. Geological Survey Borehole, Fetcham Mill, Surrey, at 750 feet depth. Upper Cretaceous (Cenomanian).

DIMENSIONS. Holotype : diameter of central body 36 by 42 μ , length of processes up to 14 μ . Range : diameter of central body 33–59 μ , length of processes up to 17 μ . Number of specimens measured, 13.

REMARKS. The processes, in the specimens possessing both gonial and sutural processes, are subconical. After further study these examples may be separated from the usual type of *H. ramosa* var. *reticulata* possessing only gonial processes. This variety is generally similar to *H. ramosa* var. *ramosa* but is readily distinguished by the reticulate surface of the central body.

H. ramosa var. *reticulata* is present in small numbers throughout the Cenomanian of England.

***Hystrichosphaera cingulata* (O. Wetzel)**

Pl. I, fig. 9

- 1933. *Cymatiosphaera cingulata* O. Wetzel : 28, pl. 4, fig. 10.
- 1954. *Hystrichosphaera cingulata* (O. Wetzel) Deflandre : 258.
- 1955. *Hystrichosphaera cingulata* (O. Wetzel) ; Deflandre & Cookson : 267, pl. 6, figs. 4, 5.
- 1963. *Hystrichosphaera cingulata* (O. Wetzel) ; Górka : 51, pl. 6, figs. 8–10.
- 1963. *Hystrichosphaera cingulata* (O. Wetzel) ; Baltes : 587, pl. 4, figs. 12–17.
- 1964. *Hystrichosphaera cingulata* (O. Wetzel) ; Rossignol : 87, text-fig. G.

DESCRIPTION. Examples of *H. cingulata* are common in the Cenomanian of England and are very similar to those described by Deflandre & Cookson (1955) and

Górka (1963). *H. cingulata* is characterized by well developed crests beyond which the gonal processes or thickenings do not protrude, the latter acting apparently only as supporting structures. The processes may be either simple or may terminate with a small bifurcation. The surface of the central body is smooth ; however the periphragm forming the crests may be slightly reticulate. The reflected tabulation is typical of the genus.

H. cingulata has a stratigraphic range from the Cenomanian (England) to the Pleistocene (Eastern Mediterranean).

MATERIAL (Figured). Geol. Surv. Colln., slide PF.3039(1). Lower Chalk, H.M. Geological Survey Borehole, Fetcham Mill, Surrey, at 730 feet depth. Upper Cretaceous (Cenomanian).

DIMENSIONS. Figured specimen : diameter of central body 37 by 39 μ , height of crests up to 13 μ . Range of Cenomanian specimens : diameter of central body 26–48 μ , height of crests up to 13 μ . Number of specimens measured, 15.

***Hystrichosphaera cingulata* var. *reticulata* nov.**

Pl. 1, fig. 10 ; Pl. 2, fig. 4

DERIVATION OF NAME. Latin, *reticulatus*, net-like—with reference to the reticulate nature of the periphragm.

DIAGNOSIS. A variety of *H. cingulata* with central body composed of smooth endophragm and strongly reticulate periphragm often somewhat thickened. Gonal "processes" not protruding above sutural crests, processes acting more or less as supporting structures for crests. Processes simple or terminating with small bifurcation.

HOLOTYPE. Geol. Surv. Colln., slide PF.3039(2). Lower Chalk, H.M. Geological Survey Borehole, Fetcham Mill, Surrey, at 730 feet depth. Upper Cretaceous (Cenomanian).

DIMENSIONS. Holotype : diameter of central body 40 by 55 μ , height of crests up to 14 μ . Range : diameter of central body 33–59 μ , height of crests up to 17 μ . Number of specimens measured, 12.

REMARKS. This variety strongly resembles *H. cingulata* (O. Wetzel) but the central body has a strongly reticulate surface. Górka (1963) states that many of the French examples of *H. cingulata* are lightly punctate and so may well belong to *H. cingulata* var. *reticulata*.

H. cingulata var. *reticulata* occurs infrequently in the Middle and Upper Cenomanian of England.

***Hystrichosphaera crassimurata* sp. nov.**

Pl. 1, fig. 11

DERIVATION OF NAME. Latin, *crassus*, thick ; *murus*, wall—with reference to the extreme thickening of the central body periphragm.

DIAGNOSIS. A species of *Hystrichosphaera* with well developed crests. Gonal processes reduced to supports for crests. Periphragm of each reflected plate area smooth and extremely thickened. Reflected tabulation typical for genus.

HOLOTYPE. Geol. Surv. Colln., slide PF.3040(1). Lower Chalk. H.M. Geological Survey Borehole, Fetcham Mill, Surrey at 670 feet depth. Upper Cretaceous (Cenomanian).

DIMENSIONS. Holotype : diameter of central body 44 by 46 μ , height of crests up to 14 μ . Range : diameter of holotype 36–46 μ , height of crests up to 14 μ . Number of specimens measured, 4.

DESCRIPTION. Only gonal processes are present and these do not extend beyond the limits of the crests. The processes are usually simple but may terminate in a small bifurcation. The periphragm of the crests is typically slightly granular whereas that of the central body is always smooth. The thickened periphragm on the central body may be up to 3.5 μ thick.

This is a rare species, recorded only from the Middle and Upper Cenomanian of England.

REMARKS. High crests enclosing the processes are present in two other species of *Hystrichosphaera* : *H. cingulata* (Wetzel) and *H. pterota* (= *Cymatiosphaera pterota* Cookson & Eisenack). However *H. crassimurata* sp. nov. is readily distinguishable from these two species by the thickened areas of the periphragm on the central body.

Hystrichosphaera crassipellis Deflandre & Cookson

Pl. I, figs. 7, 8

1954. *Hystrichosphaera crassipellis* Deflandre & Cookson, text-fig. 5.

1955. *Hystrichosphaera crassipellis* Deflandre & Cookson ; Deflandre & Cookson : 265, pl. 6, figs. 2, 3 ; text-fig. 20.

1961. *Hystrichosphaera crassipellis* Deflandre & Cookson ; Gerlach : 177, pl. 27, fig. 5 ; text-figs. 16–18.

DESCRIPTION. *H. crassipellis* possesses a thick central body wall (up to 6.5 μ in thickness) which is coarsely reticulate. The reticulation is rather irregular having from almost circular to polygonal fields. The processes are gonal, subconical in shape and commonly bifurcate with bifurcating extremities. The paired cingular processes are joined by a membrane. The crests are proximal, reasonably well developed and may be reticulate, especially at their outer edges. *H. crassipellis* is a rare species occurring throughout the Cenomanian of England.

MATERIAL (Figured). Geol. Surv. Colln., slide PF.3033(2). Lower Chalk, H.M. Geological Survey Borehole, Fetcham Mill, Surrey, at 730 feet depth. Upper Cretaceous (Cenomanian).

DIMENSIONS. Figured specimen : diameter of central body 45 by 46 μ , length of processes 12–15 μ , overall diameter 64–67 μ . Range of Cenomanian specimens :

diameter of central body $34-68\mu$, length of processes up to 26μ . Number of specimens measured, 16.

REMARKS. The Cenomanian specimens greatly resemble those of Deflandre & Cookson (1954, 1955) from the Lower Eocene of Australia, except that they are smaller. *H. crassipellis* as illustrated by Maier (1959) is very different and cannot be included within this species.

***Hystrichosphaera perforata* sp. nov.**

Pl. 5, fig. 7

DERIVATION OF NAME. Latin, *perforatus*, perforated—with reference to the perforate distal margins of the processes.

DIAGNOSIS. A species of *Hystrichosphaera* with smooth surfaced central body bearing both gonial and sutural processes. Processes either tri- or tetra-linguate, cylindrical and open with net-like perforations distally, or taeniate, being bi- or trifurcate distally. Medial branching of processes may occur. Tabulation typical of genus with plate 6" having a triangular outline.

HOLOTYPE. B.M.(N.H.) slide V.51983(1). 85 feet above base of London Clay ; Sheppey, Kent.

DIMENSIONS. Holotype : diameter of central body 40.5 by 50 , length of processes up to 26μ . Range : diameter of central body $28-50\mu$, length of processes $15-26\mu$. Number of specimens measured, 4.

DESCRIPTION. *H. perforata* sp. nov. is characterized by two types of processes : (1) gonial processes being open, cylindrical with tri- or tetra-linguate margins and possessing a triangular cross-section, and (2) taeniate processes being sutural in position. The processes are united by proximal membranes, of varying height, often with serrate edges, running along the plate boundaries. The open gonial processes are strongly fenestrate distally on the secas and occasionally along their length. A few of the processes are similar to those of *H. ramosa* var. *ramosa* in being closed distally. Each seca is usually distally bifid. The sutural processes are perforate distally where they bi- or trifurcate, and sometimes medially.

REMARKS. Two specimens of *H. ramosa* which were recorded by Gerlach (1961) possessed processes perforate distally and along their length. All the processes of these two specimens are, however, closed and the perforations are in the form of small circular holes and not net-like as in *H. perforata*. *H. porosa* (Manum & Cookson 1964) from the Upper Cretaceous of Canada possesses similar, but shorter and broader, perforate processes and a characteristic reflected tabulation—1', 5", 5c, 5''', 1''''.

***Hystrichosphaera buccina* sp. nov.**

Pl. 4, fig. 1 ; Text-figs. 10, 11

DERIVATION OF NAME. Latin, *buccina*, trumpet—with reference to the shape of the processes.

DIAGNOSIS. A species of *Hystrichosphaera* with central body composed of thick endophragm and thinner periphragm, the latter giving rise to gonal processes and

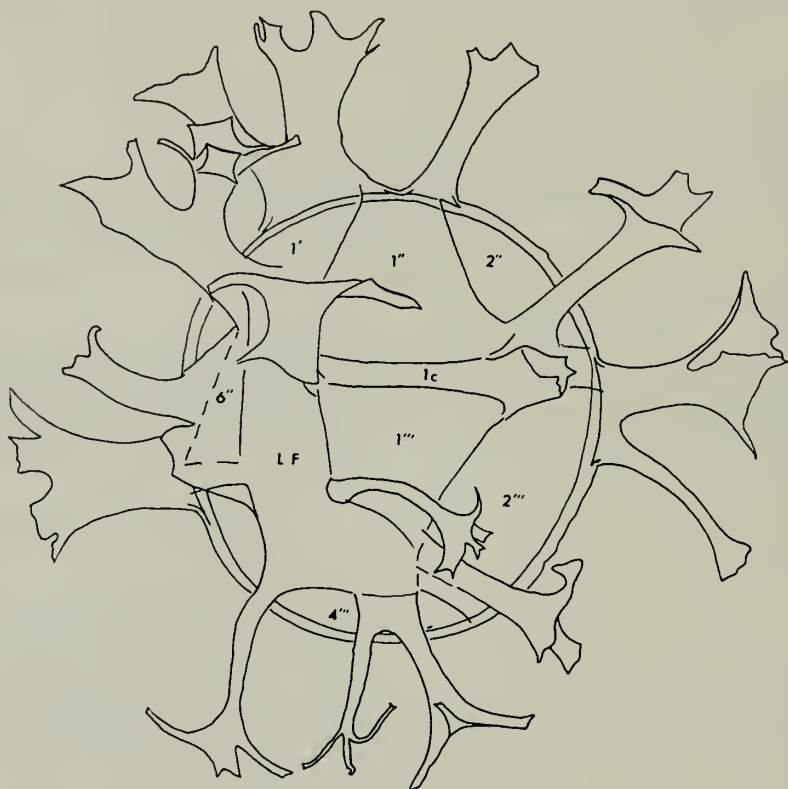


FIG. 10. *Hystrichosphaera buccina* sp. nov. Holotype, ventral view. $\times$ c.1000.

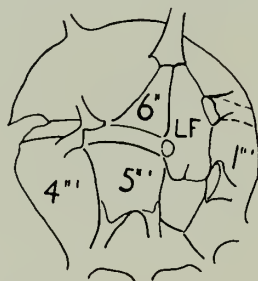


FIG. 11. *Hystrichosphaera buccina* sp. nov. A specimen from the London Clay, ventral view. $\times$ c.1000.

proximal crests. Surface of central body slightly granular or rarely reticulate. Processes only gonial, simple or branched, and always open distally. Reflected tabulation is 3-4', 6", 6c, 5''', 1''''.

HOLOTYPE. B.M.(N.H.), slide V.51989(1). 106 feet above base of London Clay ; Whitecliff Bay, Isle of Wight.

DIMENSIONS. Holotype : diameter of central body 58 by 62 μ , length of processes up to 32 μ . Range : diameter of central body 54-68 μ , length of processes 24-36 μ . Number of specimens measured, 4.

DESCRIPTION. The endophragm of the central body is 1.5-2 μ thick and the periphragm up to 1 μ . The processes terminate distally in three or more secæ, which may be patulate, flaring or recurved. The tips of the secæ may be oblate, bifid or bifurcate. This species occurs throughout the London Clay of England.

REMARKS. *H. buccina* sp. nov. is distinguished from all other species of *Hystrichosphaera*, except *H. tertiaria* (Eisenack & Gocht), by the characteristic form of the processes. *H. buccina* differs from *H. tertiaria* in the tabulation, the latter reflecting 5 precingular and 5 postcingular plates, 4 elongate rhombohedral cingular plates and a fifth triangular cingular plate. In *H. buccina* 6" is reflected and is triangular, whilst 6c runs along its antapical edge. Often the boundary between 6" and 6c is ill-defined and may only be seen at high magnification. *H. tertiaria* has only three apical plates whereas *H. buccina* may have 3 or 4. When 4 are present 1' and 4' are both narrow elongate plates and are in line with the corresponding shortened sulcus. The processes of one of the London Clay specimens are reticulate or occasionally perforate, but their form is different from that of *H. perforata* sp. nov.

Hystrichosphaera cornuta Gerlach

Pl. 4, fig. 7 ; Text-fig. 12

1961. *Hystrichosphaera cornuta* Gerlach : 180, pl. 27, figs. 10-12.

DESCRIPTION. The specimens are identical to those described by Gerlach (1961) and possess the following reflected tabulation—3-4', 6", 6c, 5''', 1p, 1''''', with plate 6" triangular in outline. Whilst some species reflect only 3 apical plates, others show an elongate division of plate 1' to give rise to two plates which are in line with the sulcus. There is occasionally an apical bulge which interrupts the otherwise regular outline of the central body and lies immediately below the apical process. Gonial and sutural processes are present, and may occasionally be open. In some individuals the large apical process possesses small lateral spines.

H. cornuta has only previously been recorded from the Middle Oligocene-Middle Miocene of N.W. Germany by Gerlach (1961).

MATERIAL (figured). B.M.(N.H.) slide V.51741(2). 85 feet above base of London Clay ; Sheppey, Kent.

DIMENSIONS. Figured specimen : diameter of central body 45 by 51μ , length of processes up to 11μ , length of apical process 25μ . Range : diameter of central body $39\text{--}52\mu$, length of processes $7\text{--}13\mu$, length of apical process $20\text{--}26\mu$. Number of specimens measured, 5.

Hystrichosphaera cornuta var. *laevimura* nov.

Pl. 4, fig. 5

DERIVATION OF NAME. Latin, *laevis*, smooth ; *murus*, wall—with reference to the smooth wall possessed by the central body in this variety.

DIAGNOSIS. A variety of *H. cornuta* (Gerlach) with smooth surfaced central body. Gonal and sutural processes short and subconical. A large distinctive apical process present often bearing small lateral spines.

HOLOTYPE. B.M.(N.H.) slide V.51752(3). 78 feet above base of London Clay ; Sheppey, Kent.

DIMENSIONS. Holotype : diameter of central body 43 by 53μ , length of processes up to 12μ . Range : diameter of central body $34\text{--}64\mu$, length of processes up to 14μ , length of apical process $16\text{--}32\mu$. Number of specimens measured, 4.

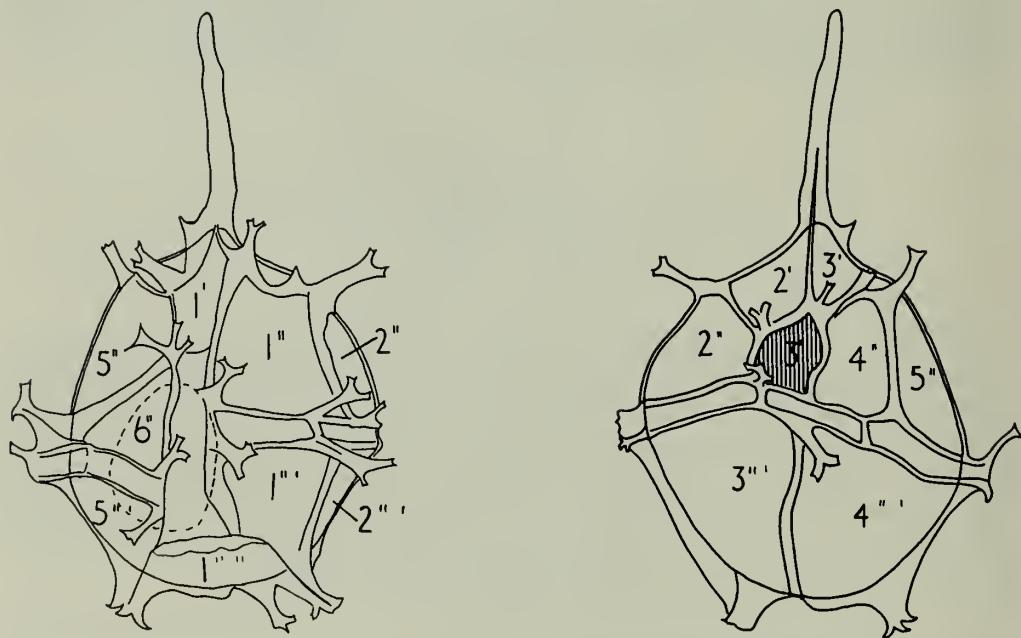


FIG. 12. *Hystrichosphaera cornuta* Gerlach. A specimen from the London Clay. Left, ventral view, plate 3" (the operculum of the archaeopyle) lying within the central body ; right, dorsal view. $\times$ c.1000.

REMARKS. *H. cornuta* var. *laevimura* nov. differs from *H. cornuta* by possessing a central body with a smooth wall and is separated from this species because of the absence of intermediate forms with slightly granular walls. The apical bulge, occasionally found in *H. cornuta*, is also found in this variety. The processes of the latter are often more slender than those of *H. cornuta* but this feature is not characteristic.

This is a rare form, only recorded from the London Clay of England.

Hystrichosphaera cf. *cornuta* Gerlach

DESCRIPTION. The central body of this form is slightly granular and bears very short gonol and sutural processes. The processes may be simple, bifurcate or trifurcate. A moderate sized apical process is present.

MATERIAL. B.M.(N.H.) slide V.51985(1). 25 feet above base of London Clay ; Whitecliff Bay, Isle of Wight.

DIMENSIONS. V.51985(1) : diameter of central body 53 by 55 μ , length of processes up to 9 μ , length of apical process 18 μ . Range : diameter of central body 31–55 μ , length of processes 4–9 μ , length of apical process 11–18 μ . Number of specimens measured, 3.

REMARKS. *H.* cf. *cornuta* from the London Clay appears to be transitional to *H. speciosa* (Deflandre 1934). The central body is less granular and the processes, particularly the apical one, are shorter than is normal in *H. cornuta*. The apical process, however, is similar in structure.

Hystrichosphaera monilis sp. nov.

Pl. 5, fig. 2

DERIVATION OF NAME. Latin, *monile*, necklace or string of beads—with reference to the appearance of the sutural crests.

DIAGNOSIS. A species of *Hystrichosphaera* possessing a spherical central body with slightly granular surface. Processes short, sub-conical to cylindrical, closed, simple or distally forked. Granules concentrated along proximal sutural crests.

HOLOTYPE. B.M.(N.H.), slide V.51986(1). 78 feet above base of London Clay ; Sheppey, Kent.

DIMENSIONS. Holotype : diameter of central body 36 by 38 μ , length of processes up to 11 μ . Range : diameter of central body 31–46 μ , length of processes up to 11 μ . Number of specimens measured, 5.

DESCRIPTION. Distally the processes may be simple, bi- tri- or tetrafurcate. When the processes are furcate, the furcations are digitate and always erect. Each taeniate furcation may be bifid or have a serrate or entire distal margin. Some of the processes are fenestrate proximally.

REMARKS. The concentration of granules along the plate boundaries, the spherical shape of the central body and the short erect processes differentiate *H. monilis* sp. nov. from all other described species of *Hystrichosphaera*.

***Hystrichosphaera* sp.**

Pl. 9, fig. 9

DESCRIPTION. A type of *Hystrichosphaera* with coarsely reticulate periphragm forming crests and processes, as well as surface of central body. The crests are well developed and bear small protruberances or stunted processes which terminate bluntly or are bifid. Gonal and a small number of sutural processes are present.

MATERIAL (figured). B.M.(N.H.), slide V.51724(1). Speeton Clay, Shell West Heslerton Borehole at 42.5 metres depth, West Heslerton, Yorkshire. Lower Cretaceous (Lower Barremian).

DIMENSIONS. Figured specimen : diameter of central body 39 by 39 μ , length of processes up to 11 μ . Second specimen : diameter of central body 43 by 51 μ , length of processes up to 10 μ .

REMARKS. This form has been encountered only rarely at one horizon, and it is characterized by its coarsely reticulate periphragm. It differs from *H. ramosa* in the reduced state of the processes and from *H. cingulata* var. *reticulata* in the presence of the latter. Since only two specimens were available for study and the presence of the typical *Hystrichosphaera* reflected tabulation was not verified. No specific name has been given.

Genus ***ACHOMOSPHAERA*** Evitt 1963 : 163

DIAGNOSIS. Test consisting of spherical to ellipsoidal central body with pre-cingular archaeopyle and furcate, spine-like processes like those of *Hystrichosphaera* in both structure and distribution, but without sutural ridges or septa connecting their bases as in that genus. Tips of processes not connected. Wall two-layered ; layers typically in close contact between bases of processes.

TYPE SPECIES. *Hystrichosphaeridium ramuliferum* Deflandre 1937.

REMARKS. One of the authors (R. J. D.) was allowed, by kind permission of Professor Deflandre, to examine the type material. One paratype, figured by Deflandre (1937, pl. 14, fig. 6), under high magnification was seen to possess very faint lines on the surface of the central body delimiting the plate boundaries. Such lines were not observed on the holotype but this was probably due to the obscuring nature of particles within the flint. These faint lines, slight thickenings of the periphragm and comparable to the sutural crests of *Hystrichosphaera*, have been observed in a number of chemically prepared specimens belonging to this genus.

TABLE 2

Species and varieties of <i>Hystrichosphaera</i>	Surface of central body	Position of processes	Type of processes	Other characteristic features	Stratigraphic range
<i>H. ramosa</i> var. <i>ramosa</i>	Smooth	Gonal $\pm$ sutural	Tapering to subconical	Proximal crests	Upper Jurassic-Eocene (Oxfordian-Ypresian)
var. <i>multibrenis</i>	Smooth or slightly reticulate	Gonal & sutural	Subconical to rudimentary, commonly $< \frac{1}{2}$ central body diameter	Proximal crests, markedly extending up processes	Lower Cretaceous-Eocene (Hauterivian-Ypresian)
var. <i>reticulata</i>	Reticulate	Gonal $\pm$ sutural	Taeniate to subconical	Proximal crests	Upper Cretaceous (Cenomanian)
var. <i>gracilis</i>	Smooth	Gonal & sutural	Slender, commonly $> \frac{1}{2}$ central body diameter	Proximal crests	Upper Cretaceous (Cenomanian)-Miocene
var. <i>granulosa</i>	Granular	Gonal & sutural	Slender, commonly $> \frac{1}{2}$ central body diameter	Proximal crests	Eocene (Ypresian)
var. <i>granomembranacea</i>	Granular	Gonal & sutural	Joined by membranes	Membranes commonly well developed in cingular regions	Eocene (Ypresian)
var. <i>membranacea</i>	Smooth	Gonal & sutural	Joined by membranes	Membranes commonly well developed in cingular and polar regions	Eocene-Pleistocene (Ypresian)
<i>Hystrichosphaera</i> sp.	Reticulate	Gonal & sutural	Processes rudimentary	Crests well developed. Processes are small protuberances	Upper Jurassic (Lower Barremian)

Species and varieties of <i>Hystriochosphaera</i>	Surface of central body	Position of processes	Type of processes	Other characteristic features	Stratigraphic range
<i>H. cingulata</i> var. <i>reticulata</i>	Reticulate	Gonal	Do not extend beyond crests	Periplasm sometimes thickened	Upper Cretaceous (Cenomanian)
<i>H. crassimurata</i>	Smooth	Gonal	Do not extend beyond crests	Periplasm greatly thickened within plate areas	Upper Cretaceous (Cenomanian)
<i>H. crassipellis</i>	Reticulate	Gonal	Subconical	Crests may be reticulate	Upper Cretaceous–Eocene (Cenomanian)
<i>H. cingulata</i>	Smooth	Gonal	Do not extend beyond crests	Crests well developed	Upper Cretaceous (Cenomanian)–Pleistocene
<i>H. perforata</i>	Smooth	Gonal & sutural	Taeniate or cylindrical	Open with net-like perforations distally	Eocene (Ypresian)
<i>H. buccina</i>	Smooth, slightly granular, or reticulate	Gonal	Cylindrical and open distally	Central body wall	Eocene (Ypresian)
<i>H. cornuta</i>	Granular	Gonal & sutural	Subconical	Large apical process	Eocene (Ypresian)–Middle Miocene
<i>H. cornuta</i> var. <i>laevimura</i>	Smooth	Gonal & sutural	Subconical	Large apical process	Eocene (Ypresian)
<i>H. cf. cornuta</i>	Slightly granular	Gonal & sutural	Simple to subconical	Short apical process	Eocene (Ypresian)
<i>H. monilis</i>	Slightly granular	Gonal & sutural	Subconical to cylindrical	Granules concentrated along sutural crests	Eocene (Ypresian)

The character and known distribution of species and varieties of the genus
Hystriochosphaera

Achomosphaera ramulifera (Deflandre)

Pl. 2, fig. 3

1935. *Hystrichosphaera* cf. *ramosa* (Ehr.) ; Deflandre, pl. 5, fig. 11.
 1937. *Hystrichosphaeridium ramuliferum* Deflandre : 74, pl. 14, figs. 5, 6 ; pl. 17, fig. 10.
 1941. *Hystrichosphaeridium ramuliferum* Deflandre ; Conrad : 2, pl. 1, fig. J.
 1948. *Hystrichosphaeridium ramuliferum* Deflandre ; Pastiels : 39, pl. 3, figs. 17-19.
 ?1952. *Hystrichosphaeridium ramuliferum* Deflandre ; W. Wetzel : 398, pl. A, fig. 9 ; text-fig. 9.
 1952. *Hystrichosphaeridium ramuliferum* Deflandre ; Deflandre, text-fig. 4.
 1955. *Hystrichosphaeridium ramuliferum* Deflandre ; Valensi : 594, pl. 4, fig. 6.
 1959. *Hystrichosphaeridium ramuliferum* Deflandre ; Gocht : 71, pl. 3, fig. 9.
 1963. *Hystrichosphaeridium ramuliferum* Deflandre ; Baltes : 586, pl. 7, figs. 13, 17, 18.
 1963. *Hystrichosphaeridium ramuliferum* Deflandre ; Górka : 59, pl. 8, fig. 3 ; text-fig. 6, figs. 3, 4.
 1963. *Baltisphaeridium ramuliferum* (Deflandre) Downie & Sarjeant : 92.
 1963. *Achomosphaera ramulifera* (Deflandre) Evitt : 163.

DESCRIPTION. Representatives of this species occur infrequently in the Cenomanian of England and are very similar to the type material. The central body is smooth or very slightly reticulate and upon it may be traced lines marking the reflected plate boundaries. The processes are hollow, often possessing rather bulbous bases, and having usually trifurcate with bifurcating extremities. The cingular processes are commonly joined and a distinctive apical process is usually present. The London Clay forms attributed to *A. ramulifera* often differ from the type material in having processes with more than three furcations, exceptionally six spines arising from one process. When six spines are present, they have apparently resulted from the elongation of the bifid tips of the three original furcations. Pastiels (1948) also recorded forms from the Ypresian of Belgium which may have more than three spines arising from a single process. The surface of the central body may be smooth or slightly granular.

The species has a stratigraphic range from the Cenomanian to the Middle Miocene.

As with *Hystrichosphaera ramosa*, *A. ramulifera* is probably divisible into a number of varieties ; one obvious variety would be those forms possessing multifurcate processes as opposed to the trifurcate processes of the type material. In the present state of knowledge, however, it is better to proceed cautiously in the erection of varieties, since too few specimens have been studied for an adequate picture to have emerged.

DIMENSIONS. Cenomanian forms : diameter of central body 40-56 μ , length of processes up to 36 μ . Number of specimens measured, 4. London Clay forms : diameter of central body 24-54 μ , length of processes up to 35 μ . Number of specimens measured, 10.

Achomosphaera ramulifera var. *perforata* nov.

Pl. 5, figs. 1, 4

DERIVATION OF NAME. Latin, *perforatus*, perforated—with reference to the perforate nature of the processes.

DIAGNOSIS. A variety of *A. ramulifera* with gonal processes fenestrate proximally and sometimes distally.

HOLOTYPE. B.M.(N.H.) slide V.51764(1). 14 feet above base of London Clay ; Whitecliff Bay, Isle of Wight.

DIMENSIONS. Holotype : diameter of central body 33 by 42 μ , length of processes 16–18 μ . Range : diameter of central body 33–56 μ , length of processes 15–26 μ . Number of specimens measured, 3.

REMARKS. The forms placed in *A. ramulifera* var. *perforata* differ from the typical *A. ramulifera* by the presence of perforate processes. This characteristic was not thought distinctive enough to justify the creation of a new species.

This variety occurs infrequently in the London Clay (Ypresian) of England.

Achomosphaera alcicornu (Eisenack)

Pl. 5, fig. 3

1954. *Hystrichosphaeridium alcicornu* Eisenack : 65, pl. 10, figs. 1, 2 ; text-fig. 5.

1961. *Hystrichosphaeridium alcicornu* Eisenack : Gerlach : 188–189, pl. 28, fig. 7.

DESCRIPTION. The London Clay specimens are very similar to *H. tertiaria* (Eisenack & Gocht) and differ only in the absence of clearly defined plate boundaries. A precingular archaeopyle is present. That the archaeopyle is precingular is determined by its shape and the presence of 5 surrounding processes. The apical process and the cingular processes are typically branched. As in all species of *Achomosphaera* only gonal processes are present. The occasional specimen in the London Clay is slightly granular and some possess processes that are perforate distally.

MATERIAL (figured). B.M.(N.H.) slide V.51765(1). Metropolitan Water Board Borehole No. 11 at 83.25 feet depth. London Clay : Enborne, Berkshire.

DIMENSIONS. Figured specimen : diameter of central body 54 by 54 μ , length of processes 28–40 μ . Range : diameter of central body 49–66 μ , length of processes 24–46 μ . Number of specimens measured, 4.

REMARKS. The stratigraphic range of *A. alcicornu* is from the Eocene (Ypresian) to the Middle Miocene (Gerlach 1961).

Achomosphaera sagena sp. nov.

Pl. 2, figs. 1, 2

DERIVATION OF NAME. Latin, *sagena*, fish-net—with reference to the distinctive net-like pattern on the surface of the central body.

DIAGNOSIS. Wall of central body extremely thick, apparently composed of columar elements, surface coarsely reticulate. Closed gonial processes hollow, trifurcate with bifurcate extremities, and commonly possessing reticulate bases. Processes sometimes branched, branching mainly confined to cingular zone. Characteristically shaped precingular archaeopyle often present.

HOLOTYPE. Geol. Surv. Colln. slide PF.3041(1). Lower Chalk, H.M. Geological Survey Borehole, Fetcham Mill, Surrey, at 650 feet depth. Upper Cretaceous (Cenomanian).

DIMENSIONS. Holotype : diameter of central body 48μ , length of processes up to 20μ . Range : diameter of central body $35\text{--}59\mu$, length of processes up to 28μ . Number of specimens measured, 8.

DESCRIPTION. The wall of the central body, which may be up to 5μ thick, is composed of elongate cellular elements lying perpendicular to the surface. The surface reticulation is coarse and may be up to 1.5μ across (Pl. 2, fig. 2).

A. sagena sp. nov. has only been recorded from the Cenomanian of England.

REMARKS. *A. sagena* is similar to *H. crassipellis* (Deflandre & Cookson) in that both possess thick walls of an identical nature with a reticulate surface. However sutural crests are absent in *A. sagena*.

Achomosphaera neptuni (Eisenack)

Pl. 3, fig. 7 ; Pl. 9, fig. 11

1958. *Baltisphaeridium neptuni* Eisenack : 399, pl. 26, figs. 7, 8 ; text-fig. 8.

1959. *Baltisphaeridium neptuni* Eisenack ; Gocht : 73, pl. 4, fig. 14

DESCRIPTION. *A. neptuni* possesses a central body with a reticulate or sometimes slightly fibrous surface. The processes are gonial in position, taeniate or taeniate-triangular and may be bifurcate or trifurcate. In the cingular zone the processes are branched. The processes are fibrous, the fibres sometimes radiating from the bases of the processes and these may be slightly thickened along the reflected plate boundaries joining the processes. A precingular archaeopyle is often present.

MATERIAL (figured). B.M.(N.H.) slides V.51716–17. Speeton Clay, Shell West Heslerton boring at 103.25 metres depth, West Heslerton, Yorkshire. Lower Cretaceous (Middle Hauterivian).

DIMENSIONS. V.51716, diameter of central body 61 by 66μ , length of processes up to 28μ . V.51717, diameter of central body 47 by 52μ , length of processes up to 21μ .

REMARKS. The Hauterivian examples strongly resemble those forms illustrated by Eisenack (1958) from the Aptian of Germany. In both of Eisenack's photographs (pl. 26, figs. 7 and 8) the views are either apical or antapical, a rather misleading orientation, the archaeopyle being seen in profile on the top side of these figures. The antapical view is shown in one of the specimens figured here, pl. 3, fig. 7, the archaeopyle being to the north-east. The processes of *A. neptuni* are very characteristic and it should be noted that they are not distally bifurcate as is usual in this genus and in *Hystrichosphaera*.

OTHER SPECIES

Achomosphaera hyperacantha (Deflandre & Cookson). This species, *Hystrichosphaera hyperacantha* Deflandre & Cookson 1955, which possesses very faint or invisible plate outlines is here considered to belong to the genus *Achomosphaera* Evitt and is renamed accordingly. Miocene ; Australia. *Achomosphaera triangulata* (Gerlach 1961 : 194, pl. 29, fig. 1) is here transferred to *Achomosphaera* on the basis of the possession of a precingular archaeopyle and the arrangement of the processes. Miocene ; Germany.

CONCLUSIONS

The characteristics and known stratigraphical distribution of the species and varieties of the genus *Hystrichosphaera* are summarized in the accompanying table (Table 2). The varieties of *H. ramosa*, as has been previously pointed out, are intergrading and, as one would expect, no clear stratigraphical picture emerges. The more distinctive species of this genus, when better known, may be of some stratigraphic value. For instance *H. crassipellis* (Deflandre & Cookson) has not been recorded from deposits earlier than the Cenomanian, nor has it been recorded from the Ypresian of England. Thus its stratigraphic range appears limited. Similarly *H. cornuta* (Gerlach) has not been recorded from deposits earlier than Tertiary.

Species of *Hystrichosphaera* are extremely rare in the Upper Jurassic, becoming more common in the Lower Cretaceous and from the Upper Cretaceous to the present day are an important constituent of the dinoflagellate cyst population. Variation has, however, been on a rather limited theme so making species differentiation extremely difficult. Moreover there appears to be a complicated plexus of evolution, particularly noticeable in the *H. ramosa* group. More detailed studies in the future may, however, throw light on some of these problems and aid the systematist and the stratigrapher.

V. THE GENUS *HYSTRICHOSPHAERIDIUM* AND ITS ALLIES

By R. J. DAVEY & G. L. WILLIAMS

INTRODUCTION

The early history of the study of fossil dinoflagellate cysts, first described by Ehrenberg (1838), is discussed in the previous chapter.

White (1842) was the first to describe the forms possessing tubular processes in his section on types of *Xanthidia tubifera*. In 1933, O. Wetzel placed all the then regarded species of fossil microplankton in the new genus *Hystrichosphaera*. Deflandre (1937) subdivided this genus separating those forms possessing an equatorial girdle and polygonal fields, which he placed in the genus *Hystrichosphaera* emend., and those without surface ornamentation which he placed in a new genus *Hystrichosphaeridium*. The diagnosis of the genus *Hystrichosphaeridium* was given as follows: "This genus comprises all the hystrichospheres totally destitute of an equatorial system of elongate plates and whose shell, in general, does not bear fields or plates limited by sutures. The shell, of dimensions greater than 20 μ , is most often spherical or spheroidal; some species, however, are more or less elongate."

Eisenack (1958) emended and restricted this genus as follows: "Hystrichospheres with spherical to oval, non-tabulate central shell and with more or less numerous, mostly well separated and in general similar appendages, the ends being open and often expanded in funnel-like fashion." Those species not included in *Hystrichosphaeridium* by Eisenack have been revised by Downie & Sarjeant (1963).

Before classification of the spiny spheres placed in the genus *Hystrichosphaeridium* Deflandre could be attempted with any precision, their affinities had to be determined. Certain organisms such as forms belonging to the genus *Gonaulacysta*, are associated with species placed in *Hystrichosphaeridium*, and have a similar two layered body-wall apparently composed of the same or a very similar organic substance. These organisms are obviously related to the dinoflagellates and are either resting or reproductive cysts. They possess a characteristic ornamentation which can be related to the theca of modern dinoflagellates; for example the crests marking the tabulation as seen in *Gonyaulacysta* and *Hystrichosphaera* or less obvious the distinctive equatorial region as possessed by *Deflandrea* or *Palaeohystrichophora*.

Thus many forms of fossil microplankton could definitely be said to be cysts of dinoflagellates, but what of the genus *Hystrichosphaeridium*? Numerous forms had been attributed to this genus but dinoflagellate features had not been definitely noted in any of them. In fact they appeared to be simple spherical shells possessing a number of randomly arranged tubular appendages, usually with an opening or pylome of some kind which no doubt was used by the organisms as an exit. It was not until 1961 that Evitt pointed out the importance of these openings. He drew attention to the fact that most of the openings had angular margins and realized that here was evidence of breakage along a definite line. These openings, or "archaeo-

pyles " as he called them, were not irregular ruptures of a cyst wall but within a species were of constant shape and size. In forms that are definitely cysts of dinoflagellates, archaeopyles are formed by the loss of areas which correspond to a single plate or plates of the original dinoflagellate theca. Four types of archaeopyle were differentiated by Evitt. They are the precingular and intercalary archaeopyles, each formed by the loss of one plate ; the apical archaeopyle formed by the loss of the apical region, commonly four plates ; and the epitrectal archaeopyle formed by the loss of the whole of the epitract above the girdle. Examination of species from the genus *Hystrichosphaeridium* reveals that the archaeopyle is practically always apical for three reasons :

- (1) Surrounding the archaeopyle, in forms possessing less than 30 processes, there are constantly six processes corresponding to six precingular plates ;
- (2) The detached operculum frequently bears four processes, reflecting the four apical plates found in many dinoflagellates ;
- (3) In ovoidal or elongate forms the archaeopyle is usually formed at one of the extremities.

It was discovered in a number of forms, for instance *H. tubiferum* (Ehrenberg), that there was an obvious circular arrangement of the processes around the central body of the cyst, and that the number of processes was equal to the number of plates possessed by forms having a typical *Gonyaulax*-type tabulation. Thus in the above forms, one process on the central body of the cyst reflects one plate in the dinoflagellate theca, the process extending from the cyst to the centre of the plate. Such processes are referred to as being intratabular and from them may be calculated the original tabulation of the dinoflagellate.

Apart from the apical archaeopyle other features may be used in the orientation of the specimen and the elucidation of the process arrangement. Although the processes may all be of the same type, the sulcal processes, like the corresponding plates, are usually relatively small in size. The antapical process and the cingular processes usually expand to some extent and terminate with a spinous or serrate margin. The spines become finer away from the process margin and it is very easy to imagine a plate affixed to such a process termination.

All the above points seem to indicate conclusively that forms belonging to the genus *Hystrichosphaeridium* are cysts of dinoflagellates. The cysts are formed within dinoflagellate thecae, during or as a response to adverse conditions, the processes acting as pillars between the cyst and the thecal wall, and holding the cyst in position. Subsequently to the cyst formation the dinoflagellate theca is lost, the latter only very rarely being observed in preserved material. Sarjeant (1965, text-fig. 3) tentatively reconstructed the original tabulation of a dinoflagellate theca from the distribution of the processes for the species, *Oligosphaeridium vasiformum* (Plate 9, fig. 7).

Evitt (1961) suggests that there were three main divisions in the genus *Hystrichosphaeridium* : those forms possessing cingular or girdle processes of similar form to the other processes, those with distinct, often more slender, cingular processes and

those forms having a cingular region devoid of processes. He concludes that the character of the cingular processes, or their absence, is of taxonomic importance and could be used in the subdivision of this genus.

During a revision of the genus *Hystrichosphaeridium* it was noticed that most of the species could be placed in well-defined groups based primarily on the type of archaeopyle, the number of processes on the apical region and the overall number of processes on the central body. Forms possessing an apical archaeopyle and one process per plate may have either one, three or four apical processes, the familiar type of *Hystrichosphaeridium* possessing four apical processes. Subdivision of this group was made on the presence or absence and type of cingular process. The genus *Hystrichosphaeridium* is emended to restrict it to forms possessing normal tubular cingular and sulcal processes. These forms possess a process arrangement reflecting a certain tabulation, that is characterized by the type species *H. tubiferum* (Ehrenberg) —4'(-5'), 6", 6c, 5-6"', 1p, 1'''' and a variable number of sulcal processes. Forms where the cingular processes are absent are placed in a new genus *Oligosphaeridium*. A third genus, *Perisseyasphaeridium* gen. nov., is erected to contain forms somewhat intermediate between the previous two genera, possessing cingular and sulcal processes not of the normal tubular type, but smaller and usually closed.

The genus *Litosphaeridium* gen. nov., is characterized by the possession of three apical processes and the absence of cingular processes. Finally in this group possessing an apical archaeopyle and one process per plate is the genus *Cordon-sphaeridium* (Eisenack) which is characterized by having an archaeopyle formed by the loss of a single apical plate.

Two new genera possessing an apical archaeopyle but more than one process per plate are erected. *Polysphaeridium* gen. nov., possesses numerous processes all of the same type (*Diphyes* is easily distinguishable by the presence of a large antapical process) and *Tanyosphaeridium* gen. nov. possesses an elongate central body and at the antapex probably 3 to 6 antapical processes.

Two new genera have been erected possessing an epitrectal archaeopyle. *Homotryblum* gen. nov. possesses tubular processes of a more or less constant size, there being three apical processes. The presence of three apical processes may indicate a relationship with *Litosphaeridium* gen. nov., however cingular and sulcal processes are well developed in *Homotryblum* whereas in *Litosphaeridium* they are absent or very reduced. The other genus possessing an epitrectal archaeopyle is *Callaiosphaeridium* gen. nov. which is represented by only one species, *C. asymmetricum* (Deflandre & Courteville). It is extremely distinctive, possessing both solid and tubular processes, one or perhaps two, apical processes and no antapical processes.

Genus *HYSTRICHOSPHAERIDIUM* Deflandre 1937 : 68

1958. *Hystrichosphaeridium* Deflandre ; Eisenack : 399, 400.

EMENDED DIAGNOSIS. Subspherical chorate cysts possessing a reflected tabulation of 4' (-5'), 6", 6c, 5-6"', 1p, 1'''' and a variable number of sulcal processes. Processes

hollow, open distally, intratabular, one process per plate area. Number of processes rarely exceeding 30. Archaeopyle apical.

TYPE SPECIES. *Xanthidium tubiferum* Ehrenberg 1838. Upper Cretaceous ; Germany.

REMARKS. The central body is composed of two membranes, an inner endophragm and an outer periphragm, the latter also comprising the processes. In contrast to the genus *Oligosphaeridium*, the genus *Hystrichosphaeridium* possesses 6 circular processes. The cavities of the processes are never in contact with the interior of the central body. The sulcal processes of this genus are often noticeably smaller than the other processes which are approximately of the same size, except for the antapical process which may be larger.

The above emendation restricts the genus *Hystrichosphaeridium* to those forms possessing the given tabulation and open processes. Other forms possessing open processes and formerly included in *Hystrichosphaeridium* have been placed in new genera according to the type of archaeopyle, the tabulation, the number and form of the processes and the shape of the central body.

Hystrichosphaeridium tubiferum (Ehrenberg)

Pl. 6, figs. 1, 2 ; Pl. 8, fig. 5 ; Pl. 10, fig. 2 ; Text-fig. 13

- 1838. *Xanthidium tubiferum* Ehrenberg, pl. 1, fig. 16.
- 1848. *Xanthidium tubiferum* Ehrenberg ; Bronn : 1375, pl. 1, fig. 16.
- 1854. *Xanthidium tubiferum* Ehrenberg ; Ehrenberg, pl. 7, fig. 48 ; pl. 37, fig. 7, no. 11.
- 1904. *Ovum hispidium* (*Xanthidium tubiferum*) Ehrenberg ; Lohmann : 21.
- 1933. *Hystrichosphaera tubifera* (Ehrenberg) O. Wetzel : 40, pl. 4, fig. 16.
- 1937. *Hystrichosphaeridium tubiferum* (Ehrenberg) Deflandre : 68. (The specimens figured are of *H. recurvatum*.)
- 1940. *Hystrichosphaeridium tubiferum* (Ehrenberg) ; Lejeune-Carpentier : 218, figs. 1-4.
- 1941. *Hystrichosphaeridium tubiferum* (Ehrenberg) ; Conrad, pl. 1F, fig. 2F.
- 1952. *Hystrichosphaeridium tubiferum* (Ehrenberg) ; Gocht, pl. 1, fig. 4.
- 1963. *Hystrichosphaeridium tubiferum* (Ehrenberg) ; Górka : 55, pl. 8, figs. 1, 2 ; text-pl. 6, figs. 1, 2.

EMENDED DIAGNOSIS. Central body spherical to subspherical, smooth or slightly granular wall composed of two layers. Processes well developed, tubiform, open distally with entire or serrate circular margin. Processes give a reflected tabulation of 4-5', 6", 6c, 5-6"', 1p, 1'''' and a variable number of sulcal plates, commonly 4-5. Apical archaeopyle usually present.

HOLOTYPE. Slide XXV in a series of flints from Delitzsch, Institut für Paläontologie u. Museum der Humboldt-Universität, Berlin.

DIMENSIONS. Holotype: diameter of central body 33 by 34 μ , length of processes 27-29 μ , number of processes 24. Paratype : diameter of central body 33 by 36 μ , length of processes 19-22 μ .

DESCRIPTION. Central body composed of thin smooth endophragm and smooth or slightly granular periphragm, the latter also forming the processes. The processes are tubiform with distally a denticulate to serrate circular margin. At the base of each process is a characteristic circular mark caused by the initial divergence of the endophragm and periphragm. The processes, up to 30 in number, are usually shorter in length than the small diameter of the central body. They are of unequal width, the sulcal processes being finer and usually shorter. Lejeune-Carpentier (1940), after examination of the type material, records that this species is common from the Upper Turonian and Senonian.

The processes of the London Clay specimens often possess unusual foliaceous outgrowths emanating from the margin and these may be diagnostic enough to differentiate Eocene forms from Upper Cretaceous forms. All the London Clay forms have at least 20 processes. 10 specimens were measured, the diameter of the central body being $28\text{--}53\mu$ and length of processes $13\text{--}29\mu$.

H. tubiferum is uncommon in the Cenomanian of Fetcham Mill (Surrey) and is rather variable in the form of its processes. Specimens which closely resemble the holotype have been observed, the sulcal processes, however, being less noticeably small. At the base of the Cenomanian the processes of *H. tubiferum* expand distally and terminate in a denticulate margin, a few short secæ are often present. Towards the top of the Cenomanian the processes do not expand so much and the secæ are more pronounced and isolated. Diameter of central body $30\text{--}51\mu$, length of processes $15\text{--}37\mu$, 26 specimens being measured.

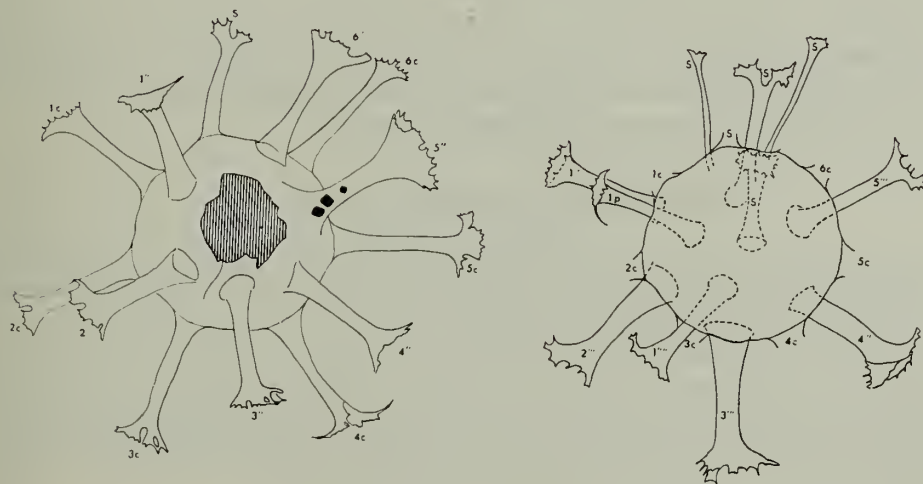


FIG. 13. *Hystrichosphaeridium tubiferum* (Ehrenberg). A specimen from the London Clay. Left, apical view showing the archaeopyle, precingular and cingular processes, and a single sulcal process; right, antapical view (by transparency) showing the precingular, sulcal, posterior intercalary and antapical processes. $\times c. 1000$.

DISCUSSION. *H. tubiferum* has been recorded many times but often incorrectly. The specimens figured by Reade (1839, pl. 9, figs. 6, 19) and Deflandre (1937, pl. 12, fig. 14 ; pl. 13, figs. 2, 14) show all the characteristics of *Hystrichosphaeridium recurvatum* (White) and should be regarded as attributable to this species. *H. tubiferum* (Valensi, 1955, pl. 4, fig. 2 ; pl. 5, fig. 8) may also belong to *H. recurvatum*.

The specimens illustrated by Eisenack (1958, pl. 25, fig. 16) and Pocock (1962, pl. 15, fig. 230) should probably be referred to *Oligosphaeridium complex* (White).

A number of other specimens have been referred to *H. tubiferum* but their true systematic position is doubtful, and almost certainly they do not belong to this species.

***Hystrichosphaeridium tubiferum* (Ehrenberg) var. *brevispinum* nov.**

Pl. 10, fig. 10

DERIVATION OF NAME. Latin, *brevis*, short ; *spina*, spine—referring to the short processes.

DIAGNOSIS. A variety of *Hystrichosphaeridium tubiferum* with processes rarely exceeding one-third of the diameter of the central body.

HOLOTYPE. B.M.(N.H.) slide V.51738(1). Metropolitan Water Board Borehole No. 39, at 160 feet depth, London Clay ; Enborne, Berkshire.

DIMENSIONS. Holotype : diameter of central body 32 by 36 μ ; length of processes up to 11 μ ; width of processes up to 11 μ ; number of processes 23. Range : diameter of central body 31–53 μ ; length of processes 6–11 μ ; width of processes up to 13 μ ; number of specimens measured, 7.

REMARKS. This variety forms a distinct group distinguishable from *Hystrichosphaeridium tubiferum* only by the length of the processes. It differs from ?*Hystrichosphaeridium arundum* (Eisenack & Cookson 1960) from the Lower Cretaceous of Australia, by having much broader processes.

***Hystrichosphaeridium deanei* sp. nov.**

Pl. 6, figs. 4, 8

DERIVATION OF NAME. Named in honour of H. Deane, an early worker on fossil microplankton from the Chalk of England.

DIAGNOSIS. Subspherical to ovoidal central body composed of thin smooth endophragm and smooth or slightly granular periphragm, the latter forming the processes. Tubular processes varying considerably in shape, sub-conical, lagenate or tubiform, open distally with entire or serrate margins. Width of processes extremely variable. Apical archaeopyle usually present.

HOLOTYPE. Geol. Surv. Colln. slide PF.3030(1). Lower Chalk, H.M. Geological Survey Borehole, Fetcham Mill, Surrey, at 690 feet depth. Upper Cretaceous (Cenomanian).

DIMENSIONS. Holotype : diameter of central body 46 by 47μ ; width of antapical process 31μ , length 35μ ; length of other processes 15 – 30μ . Number of processes 21 . Range : diameter of central body 41 – 54μ , length of processes 15 – 45μ . Number of specimens measured, 9 .

DESCRIPTION. The endophragm of the processes may be fibrous, but not strongly so. The processes vary greatly in size and shape, this variation being continuous between extremes of the range. The width of the processes on a specimen may vary from 1.5μ to 35μ ; the length of the processes is, however, more constant. The largest process is usually the antapical, it being sub-conical to lagenate in shape. In one specimen only a few of the larger processes are seen to give rise to two or three parallel branches distally. The processes reflect a tabulation of $4'$, $6''$, $6c$, $5'''$, $1p$, $1''''$ and 2 – $4s$.

H. deanei has been recorded from the Middle and Upper Cenomanian of Fetcham Mill, Surrey.

REMARKS. *H. deanei* sp. nov. resembles *H. stellatum* (Maier) recorded from the Albian and Cenomanian of Australia by Cookson & Eisenack (1962b). It is similar in the general form of the processes and the size of the central body, but the sub-conical to lagenate processes, common in the British forms, appear to be absent. The Australian form of *H. stellatum* does not appear to be comparable to Maier's type material from the Oligocene of Germany.

The form and the distal margins of the processes differentiate *H. deanei* from *H. tubiferum*. The reflected tabulation, however, reveals a fairly close relationship between the two species.

***Hystrichosphaeridium simplicispinum* sp. nov.**

Pl. 9, fig. 3

DERIVATION OF NAME. Latin, *simplicis*, simple or straight and *spinous*, thorny—referring to the rather simple nature of the processes.

DIAGNOSIS. Spherical central body composed of thin smooth endophragm and periphragm, the latter forming the processes. Processes varying considerably in size and are simple, tubiform, splaying out distally and terminate with denticulate or secate margin. A number of fine sulcal processes. Apical archaeopyle usually present.

HOLOTYPE. B.M.(N.H.) slide V.51729(2). Speeton Clay, Shell West Heslerton Borehole No. 1, Yorkshire at 39 metres depth. Lower Cretaceous (Middle Barremian).

DIMENSIONS. Holotype : diameter of central body 36 by 43μ , length of processes 17 – 26μ . Number of processes 23 , plus 4 fine sulcal processes. Range : diameter of central body 34 – 57μ , length of processes 8 – 31μ . Number of specimens measured, 4 .

DESCRIPTION. The smooth periphragm of the central body and processes is sometimes slightly perforate but more commonly smooth. At the base of each process there is a characteristic thickening of the endophragm, which is here reticulate. Only four well preserved specimens have been observed, the number of wide tubular processes ranging from 22 to 24, with 1 to 6 fine sulcal processes. The antapical process is often distinctly wider than the other processes. The reflected tabulation appears to be comparable to *H. tubiferum*.

H. simplicispinum sp. nov. is present throughout the Barremian of Yorkshire.

REMARKS. In general appearance *H. simplicispinum* strongly resembles *Cordosphaeridium eoinodes* but the fibrous periphragm is absent and the number of processes is greater.

The reflected tabulation of *H. simplicispinum* is probably the same as *H. tubiferum*, but they differ in that the processes of the former are considerably more divided and not so expanded distally.

***Hystrichosphaeridium patulum* sp. nov.**

Pl. 10, fig. 5

DERIVATION OF NAME. Latin, *patulus*, broad and spreading—with reference of the larger processes.

DIAGNOSIS. Spherical to sub-spherical central body, not exceeding 25μ in diameter, possessing a smooth thin wall and bearing two types of processes. Both types of same length and considerably expanded distally, one type much wider than the other. Distal margin entire and undulating. Length of processes one-quarter to one-half of the diameter of central body. Apical archaeopyle present.

HOLOTYPE. B.M.(N.H.) slide V.51739(1). 7 feet above base of London Clay ; Whitecliff Bay, Isle of Wight.

DIMENSIONS. Holotype : diameter of central body 11.5 by 14.5μ , length of processes up to 5.5μ , number of processes 25. Range : diameter of central body $11-19\mu$, length of processes $4-9\mu$. Number of specimens measured, 8.

DESCRIPTION. This species is characterized by its broad open processes, approximately 2μ wide, and by the finer processes, up to 1μ wide. The processes are tubiform with considerably expanded distal extremities measuring up to 7μ across. The number of processes can be up to 25. The apical archaeopyle has straight edges obviously reflecting plate boundaries.

REMARKS. The small size of this species and the two types of processes are characteristic. Its processes resemble shortened and sometimes widened processes of *H. tubiferum*, and the number present is also similar. Some relationship may perhaps be inferred between these two species.

***Hystrichosphaeridium arborispinum* sp. nov.**

Pl. 9, figs. 5, 10

DERIVATION OF NAME. Latin, *arbor*, tree ; *spinus*, spine—with reference to the tree-like appearance of the processes.

DIAGNOSIS. Sub-spherical to ovoidal central body composed of thin endophragm and granular or reticulate periphragm. Processes, composed of periphragm, hollow, tubiform, usually simple, expanding distally and terminating with complicated secate margin. Apical archaeopyle commonly present.

HOLOTYPE. B.M.(N.H.) slide V.51727(3). Speeton Clay, Shell West Heslerton Borehole No. 1, Yorkshire at 39 metres depth. Lower Cretaceous (Middle Barremian).

DIMENSIONS. Holotype : diameter of central body 39 by 39 μ , length of processes 10–19 μ . Range : diameter of central body 31–43 μ , length of processes 10–23 μ . Number of specimens measured, 4.

DESCRIPTION. The distal extremities of the processes have a distinctive ragged appearance due to the irregular shape of the secæ—some being irregularly lobate, others giving off spines laterally. Specimens with fibrous processes, and more rarely with fenestrate processes, have been observed. An apical archaeopyle commonly seems to be present, but its precise nature is difficult to determine for the specimens are extremely thin walled and easily distorted. The number of processes seems to be standardized at 22 to 23, and this together with their arrangement on the surface of the central body indicate that *H. arborispinum* sp. nov. has a reflected tabulation similar to that of *H. tubiferum*.

This species has been recorded only from the Lower and Middle Barremian of Yorkshire.

REMARKS. The form of the distal extremities of the processes characterizes this species and distinguishes it from all other described species.

H. arborispinum is basically of the same type as *H. tubiferum* (Lejeune-Carpentier 1940) but has slightly broader processes which are distally much more divided.

***Hystrichosphaeridium salpingophorum* (Deflandre)**

Pl. 10, fig. 6

1935. *Hystrichosphaera salpingophora* Deflandre : 232, pl. 9, fig. 1.
 1937. *Hystrichosphaeridium salpingophorum* (Deflandre) Deflandre : 80, pl. 13, figs. 1, 3.
 1940. *Hystrichosphaeridium salpingophorum* (Deflandre) ; Lejeune-Carpentier : 219, text-fig. 8.
 1947. *Hystrichosphaeridium salpingophorum* (Deflandre) ; Deflandre, text-fig. 1, no. 7.
 ?1948. *Hystrichosphaeridium salpingophorum* (Deflandre) ; Pastsils : 37, pl. 3, figs. 3–7.
 ?1952. *Hystrichosphaeridium salpingophorum* (Deflandre) ; W. Wetzel : 399, text-fig. 11.
 ?1952. *Hystrichosphaeridium salpingophorum* (Deflandre) ; Gocht, pl. 1, fig. 19 ; pl. 2, fig. 20.
 1952. *Hystrichosphaeridium salpingophorum* (Deflandre) ; Deflandre, text-fig. 11.
 1955. *Hystrichosphaeridium salpingophorum* (Deflandre) ; Deflandre & Cookson : 271, pl. 2, fig. 9.
 ?1958. *Hystrichosphaeridium salpingophorum* (Deflandre) ; Eisenack : 401, pl. 27, figs. 5, 6.

EMENDED DIAGNOSIS. Central body spherical to ovoidal with characteristic reflected tabulation of 4', 6'', 6c, 5''', 1p, 1'''' with variable number of sulcal processes. Processes well developed, tubiform, with sub-quadrate distal openings. Distal margins entire or denticulate. Number of processes present 25 to 30. Apical tetratabular archaeopyle practically always present.

HOLOTYPE. Slide AJ56, Laboratoire de Micropaléontologie, École Pratique des Hautes Études, Paris. Senonian ; France.

MATERIAL (Figured). B.M.(N.H.) slide V.51734(1). 146 feet above base of London Clay ; Whitecliff Bay, Isle of Wight.

DIMENSIONS. Range of specimens from type material (Deflandre 1937) ; diameter of central body 35 to 40 μ , length of processes 25 to 30 μ , the number of processes is approximately 30. Range of London Clay specimens : diameter of central body 30–44 μ , length of processes 14–20 μ . Number of specimens measured, 4.

DESCRIPTION. The surface of the central body may be smooth or slightly granular, and composed of two layers, the endophragm and periphragm (absent beneath the processes). The processes expand gradually towards the distal sub-quadrate opening, which is up to 18 μ across in the London Clay forms. Medially the processes rarely exceed 10 μ and are usually much less. The wall of the processes (composed of periphragm) is slightly fibrous. The distal margin can be serrate, undulose or even aculeate. Processes may be perforate distally.

REMARKS. The London Clay specimens have rather short and broader processes than the holotype and are perhaps a variety of *H. salpingophorum*. The ribs, illustrated by Klement (1960), extending along the length of the processes and running into the central body have not been observed. The specimen figured by Lejeune-Carpentier (1940, text-fig. 8) is very similar to the London Clay forms.

H. salpingophorum (London Clay) is generally easily distinguished from *H. tubiferum*. However certain specimens from the London Clay are transitional, often showing the circle formed at the junction of the processes and the endophragm. A close relationship with *H. tubiferum* is also indicated by the identical tabulation and intratabular processes.

The Jurassic forms formerly attributed to *H. salpingophorum* are transferred below to *Hystrichosphaeridium costatum* sp. nov.

Hystrichosphaeridium costatum sp. nov.

Pl. 10, fig. 4

- ?1938. *Hystrichosphaeridium salpingophorum* (Deflandre) ; Deflandre : 186, pl. 10, figs. 1–3.
- ?1947. *Hystrichosphaeridium salpingophorum* (Deflandre) ; Deflandre, text-fig. 1, no. 6.
- ?1952. *Hystrichosphaeridium salpingophorum* (Deflandre) ; Deflandre, text-fig. 10.
- 1960. *Hystrichosphaeridium salpingophorum* (Deflandre) ; Klement : 55, pl. 7, figs. 3–5 ; text-fig. 31.
- 1960. *Hystrichosphaeridium salpingophorum* (Deflandre) ; Sarjeant : pl. 13, fig. 7.
- 1961. *Hystrichosphaeridium salpingophorum* (Deflandre) ; Sarjeant : 99, pl. 15, fig. 7.

DERIVATION OF NAME. Latin, *costa*, rib—referring to the thickenings of the periphragm.

DIAGNOSIS. Subspherical central body possessing a moderate number of fibrous tubiform processes having sub-quadrate distal openings. Distal margin denticulate with small number of recurved prolongations. Thickened ribs extending from some of the angles of the distal margins along length of processes and onto central body surface where they connect with similar ribs extending from neighbouring processes, forming mesh-like structure. Apical archaeopyle usually present.

HOLOTYPE. B.M.(N.H.) slide V.51708, from G.R. 053890, Scarborough Castle, Yorkshire. Oxford Clay (*Quenstedtoceras mariae* Zone).

DIMENSIONS. Holotype : diameter of central body 47 by 47 μ , length of processes 19–28 μ , number of processes 24.

DESCRIPTION. The surface (periphragm) of the central body is granular or slightly reticulate. The tubiform processes have broad bases, and splay out distally in an angular fashion, their width not exceeding 9 μ medially. At the angles of the margin are commonly situated small prolongations or spines, occasionally up to 8 μ long but usually considerably smaller. The processes vary considerably in width, from 1 to 9 μ when measured medially. Only one or two finer processes are present on a specimen and these are probably sulcal processes. An occasional deeply furcate process has been observed in the central region of the cyst, these undoubtedly being cingulum processes. The ribs (thickenings of the periphragm) are very characteristic and form upon the surface of the central body a subpolygonal mesh-like arrangement, somewhat simulating the tabulation seen in the genus *Hystri-chosphaera*, but certainly not analogous to it. An apical archaeopyle is usually present, and the reflected tabulation appears to be that typical for this genus. *Hystri-chosphaeridium costatum* sp. nov. has been recorded from the Oxfordian of England, France and Germany.

REMARKS. Deflandre (1938) described *H. salpingophorum* from the Oxfordian noting the ribbed processes and an apparent similarity to the Upper Cretaceous form of this species. However, ribbing on the surface of the central body was not remarked on or shown in his illustrations (pl. 10, figs. 1–3). These forms possibly belong to *H. costatum*.

Klement (1960) described and figured specimens identical to those found in the British Oxfordian, possessing the characteristic thickenings of the periphragm.

The specimen illustrated by Lejeune-Carpentier (1940, text-fig. 7) from the Upper Cretaceous, has vague polygonal markings on the surface of the central body, but definite ribs are absent.

Sarjeant (1960, 1961) illustrated specimens of *H. costatum* as *H. salpingophorum* ; his figured specimen (1961, pl. 15, fig. 7) has been selected as holotype of the new species.

Hystrichosphaeridium readei sp. nov.

Pl. 6, fig. 3

?1940. *Hystrichosphaeridium salpingophorum* (Deflandre) ; Lejeune-Carpentier : 219, text-fig. 7.

?1940. *Hystrichosphaeridium tubiferum* (Ehrenberg) ; Lejeune-Carpentier : 218, text-fig. 5.

DERIVATION OF NAME. Named in honour of the Reverend J. B. Reade who was the first to describe and figure (1839) hystrichospheres from English flints of the Upper Cretaceous age.

DIAGNOSIS. Spherical to subspherical central body composed of smooth endophragm and periphragm. Processes, composed of the latter, slightly fibrous, cylindrical and open. Larger processes with two thickenings of periphragm extending along their length over surface of central body and joining up with similar thickenings from neighbouring processes. Processes varying in width and expanding distally, terminating in fairly complicated aculeate or secate margin. Apical archaeopyle usually present.

HOLOTYPE. Geol. Surv. Colln. slide PF.3030(2). Lower Chalk, H.M. Geological Survey Borehole, Fetcham Mill, Surrey, at 690 feet depth. Upper Cretaceous (Cenomanian).

DIMENSIONS. Holotype : diameter of central body 41 by 45 μ , length of processes 23–29 μ , number of processes 24. Range : diameter of central body 31–54 μ , length of processes 20–35 μ . Number of specimens measured, 8.

DESCRIPTION. The most characteristic feature of this species is the presence of thickenings or ribs in the periphragm. These ribs are close together near the distal end of the process and gradually diverge proximally, before separating completely on the surface of the central body, each rib passing to a different neighbouring process. Thus triangular and polygonal networks are seen on the surface of the central body. The sulcal processes are usually noticeably finer than the others and are very occasionally joined by septa, as seen in the holotype. The septa are probably modified ribs. An apical archaeopyle is usually present. The number of processes in the specimens observed varied between 23 and 27. The reflected tabulation is difficult to determine but it is probably comparable to *H. tubiferum* i.e. 4', 6", 6c, 5''', 1p, 1'''' and xs.

H. readei sp. nov. occurs in the Upper Cenomanian at Fetcham Mill, Surrey and has not been recorded lower in the succession at this locality.

REMARKS. The Cenomanian species strongly resembles and is undoubtedly related to, *H. costatum* from the Upper Jurassic. The only apparent difference between the species is in the extremities of the processes. In *H. costatum* the extremities are simply denticulate with a small number of spines, whereas in *H. readei* the extremities are considerably more complex.

H. tubiferum (Ehrenberg) as illustrated by Lejeune-Carpentier (1940, text-fig. 5), from Upper Cretaceous flint, is extremely similar to *H. readei* and could well belong to the present species.

***Hystrichosphaeridium radiculatum* sp. nov.**

Pl. 7, fig. 8 ; Pl. 9, fig. 6

DERIVATION OF NAME. Latin, *radicula*, small root—with reference to the fibres radiating from the bases of the processes.

DIAGNOSIS. Spherical to sub-spherical central body composed of reticulate endophragm and fibrous periphragm. Processes, approximately 30 in number, composed of periphragm, fibrous, mainly hollow and open distally, simple tubiform or dividing into 2 or 3 sub-parallel branches. Processes expanding slightly distally, extremities of processes entire or denticulate.

HOLOTYPE. Geol. Surv. Coll. slide PF.3031(1). Lower Chalk, H.M. Geological Survey Borehole, Fetcham Mill, Surrey, at 690 feet depth. Upper Cretaceous (Cenomanian).

DIMENSIONS. Holotype : diameter of central body 36 by 37 μ , length of processes 13–17 μ . Range : diameter of central body 31–37 μ , length of processes 11–17 μ . Number of specimens measured, 4.

DESCRIPTION. The reticulate endophragm appears to be granular at first sight before examination in detail. Along the lengths of the processes run fibrous strands which continue on to the surface of the central body and are sometimes continuous with similar strands from neighbouring processes. The depth of the furcation of the processes varies considerably, from merely a slight distal furcation to where there appears to be two separate processes in close proximity. A rather elongate apical archaeopyle is present surrounded by 6 precingular processes. The distribution of the remainder of the processes is difficult to determine precisely.

This species is uncommon and has only been identified from the Upper Cenomanian.

REMARKS. *H. radiculatum* sp. nov. is closely related to *H. mantelli* differing in that the branched processes are more common and the fibrils of the processes continue across the surface of the central body. The reflected tabulation of the two species is probably very similar.

Hystrichosphaeridium cf. *clavigerum* (Deflandre) as illustrated by Lejeune-Carpentier (1940, text-fig. 9), resembles *H. radiculatum* in size, form of the processes, and the fibrous periphragm on the surface of the central body. However, the branching processes characteristic of *H. radiculatum*, are absent.

Hystrichosphaeridium mantelli sp. nov.

Pl. 6, fig. 6

DERIVATION OF NAME. In honour of the geologist and microscopist Gideon Algernon Mantell, who did much pioneer work in interpreting the structure of Upper Cretaceous microplankton during the mid-nineteenth century.

DIAGNOSIS. Spherical to sub-spherical central body composed of thin endophragm and granular or finely reticulate periphragm.Periphragm of processes slightly fibrous. Processes predominantly simple, tubiform, buccinate or bulbous, open distally with digitate or foliate margin. Occasionally narrow, solid, closed processes occur. Number of processes 26 or less, one process per plate area. Apical archaeopyle usually present.

HOLOTYPE. Geol. Surv. Colln. slide PF.3032(1). Lower Chalk, H.M. Geological Survey Borehole, Fetcham Mill, Surrey, at 840 feet depth. Upper Cretaceous (Cenomanian).

DIMENSIONS. Holotype : diameter of central body 41 by 42 μ , length of processes 13–21 μ , number of processes 25. Range : diameter of central body 36–45 μ , length of processes 13–26 μ . Number of specimens measured, 6.

DESCRIPTION. At first sight the periphragm of the central body appears to be fairly heavily granular, but on closer examination the granules apparently result from a fine reticulation. The processes are erect and extremely variable in form, being tubiform, buccinate or even bulbous, usually open but occasionally closed, and simple or branched distally. The closed processes are extremely narrow, less than 1 μ , and solid distally. An apical archaeopyle appears always to be present. The processes give a reflected tabulation of 6", 6c, 5"', 1p, 1'''' and a variable number of sulcal processes, commonly 4–6. The detached apical region has not yet been identified.

This species has been found only in the Lower Cenomanian and is extremely uncommon.

REMARKS. The reticulate nature of the central body and the fibrous processes differentiate *H. mantelli* sp. nov. from most other species. *H. radiculatum* sp. nov. is, however, fairly similar but the processes are more deeply divided, there often being 2 to 3 sub-parallel branches, and narrower.

Hystrichosphaeridium latirictum sp. nov.

Pl. 10, fig. 8

DERIVATION OF NAME. Latin, *lati*, wide and *rictum*, open mouth—with reference to the considerably expanded distal margins of the processes.

DIAGNOSIS. Central body ellipsoidal, with smooth or slightly granular wall up to one-quarter μ thick. Processes slender, tubiform, slightly fibrous, expanding considerably distally. Processes open distally and margin circular or quadrate.

HOLOTYPE. B.M.(N.H.) slide V.51740(1). Metropolitan Water Board Borehole No. 11 at 43·25 feet depth, London Clay ; Enborne, Berkshire.

DIMENSIONS. Holotype : diameter of central body 18 by 19·5 μ , length of processes 9–12·5 μ , breadth of processes up to 2 μ , length of acuminate processes 6–8 μ , number of processes 25 (and two acuminate processes). Range : diameter of central body 11–20 μ , length of processes 6–13 μ . Number of specimens measured, 5.

DESCRIPTION. The processes show a variation in outline and nature of distal margin which can be circularly to ovoidal, serrate, undulose or aculeate. The distal extremities of the processes are usually considerably expanded, up to 13 μ wide. The length of the processes vary from one-third to two-thirds of the diameter of the central body. Besides the tubiform process there is quite often a small number of short, closed processes, as on the holotype. The latter are undoubtedly sulcal processes. An apical archaeopyle is present surrounded by 6 processes, the reflected tabulation probably being that of this genus.

H. latirictum sp. nov. has been recorded from the London Clay of Enborne and of Whitecliff Bay, Isle of Wight.

REMARKS. The size of *H. latirictum* sp. nov., in combination with the tubiform processes, is quite characteristic. *Polysphaeridium paulinae* from the Middle Jurassic of France (Valensi 1953) is similar in form but smaller with more processes, the processes being not greater than one-third of the diameter of the central body. It is possible that this species may result from misinterpretation of representatives of the genus *Stephanelytron* : the holotype, kindly lent by Prof. Deflandre for examination (in 1962), is at depth in flint and cannot be seen in full detail. Hystrichospheres with tubular processes are not otherwise known from the Middle Jurassic.

Hystrichosphaeridium recurvatum (White)

- 1839. *Xanthidium tubiferum* (Ehr.) : Reade, pl. 9, figs. 6, 9.
- 1842. *Xanthidium tubiferum palmatum* White : 39, pl. 4, div. 3, fig. 12.
- 1844. *Xanthidium tubiferum palmatum* White ; White, pl. 8, fig. 11.
- 1848. *Xanthidium palmatum* White ; Bronn : 1375.
- 1851. *Spiniferites palmatus* (White) Mantell : 251, text-fig. 79.
- ?1934. *Hystrichosphaera tubifera* (Ehr.) ; Deflandre, text-fig. 11.
- 1935. *Hystrichosphaera tubifera* (Ehr.) ; Deflandre : 15, pl. 7, fig. 10, ?11.
- 1937. *Hystrichosphaeridium tubiferum* (Ehr.) ; Deflandre : 96, pl. 13, fig. 2 ; (pl. 12, fig. 14 ; pl. 13, fig. 4).
- ?1940. *Hystrichosphaeridium recurvatum* (White) Lejeune-Carpentier : 221, text-fig. 6.
- ?1955. *Hystrichosphaeridium tubiferum* (Ehr.) ; Valensi : 592, pl. 4, fig. 2 ; pl. 5, fig. 8.
- ?1963. *Hystrichosphaeridium recurvatum* (White) ; Górka : 57, pl. 8, fig. 8 ; text-pl. 6, fig. 5.
- 1964. *Hystrichosphaeridium recurvatum* (White) ; Sarjeant : 173.

EMENDED DIAGNOSIS. Sub-spherical central body with moderate number of slender tubiform processes. Length of latter between that of radius and diameter of central body. Processes open distally, terminating with a few short orthogonal or recurved spines.

NEOTYPE. Slide AJ97, Laboratoire de Micropaléontologie, École Pratique des Hautes Études, Paris. (Figured by Deflandre 1935, pl. 7, fig. 10.) Senonian flint from the Paris Basin.

DIMENSIONS. Holotype (measured from the illustration) : diameter of central body 32 by 25 μ , maximum overall diameter 75 μ , length of processes 18–30 μ , number of processes, 25.

DESCRIPTION. The periphragm of the central body is smooth or slightly granular and of the processes is smoother or somewhat fibrous. The processes on a specimen do not vary a great deal in their length or width, the sulcal processes not being significantly smaller. Each process has constant width along its length, widening slightly at the base but not distally, where it terminates in a rosette of short spines. An apical archaeopyle is usually present. The reflected tabulation appears to be 4', 6", 6c, 5''', 1p, 1'''' and 3–6s, and so *H. recurvatum* is provisionally placed in the genus *Hystrichosphaeridium*.

H. recurvatum has only been recorded with certainty from the Senonian of Europe.

REMARKS. Sarjeant (1964a), in a paper on nomenclatural problems, pointed out that on the principle of priority the correct name for this species is *H. palmatum* and not *H. recurvatum*. White (1842) referred to this species in the text as *Xanthidium recurvatum* or *palmaforme* and in the plate caption as *X. palmatum*. Thus three alternative names were suggested. Bronn (1848) was next to refer to this species, and listed it as *X. palmatum*. In 1939 a junior homonym to the latter was proposed by Deflandre & Courteville, this later being transferred to the genus *Baltisphaeridium* (Downie & Sarjeant 1963).

Lejeune-Carpentier (1940), overlooking the work of Bronn, described this species under the name of *H. recurvatum*. Subsequent workers have followed Lejeune-Carpentier and used *H. recurvatum* as the specific name instead of the correct *H. palmatum*. Downie & Sarjeant (1964) similarly use *H. recurvatum*. Since the latter is in general use and *H. palmatum* (White) Bronn has a junior homonym, it is proposed that *H. recurvatum* should be retained as the designation for this species.

A thorough search has been made to find the holotype of *H. recurvatum* from the British Senonian, figured by White (1842), but without success. It has therefore been necessary to propose a neotype for this species. The neotype proposed was first figured by Deflandre (1935, pl. 7, fig. 10) as *Hystrichosphaera tubifera* and comes from the Senonian of France (Paris Basin).

Hystrichosphaeridium sheppeyense sp. nov.

Pl. 11, fig. 3

1955. *Hystrichosphaeridium recurvatum* (White) ; Deflandre & Cookson : 269, pl. 1, fig. 11.

1961. *Hystrichosphaeridium recurvatum* (White) ; Evitt : 391, 395, pl. 4, figs. 3–5 ; pl. 5, fig. 8.

DERIVATION OF NAME. Named after the type locality, the Isle of Sheppey, Kent.

DIAGNOSIS. Ovoidal central body with smooth or slightly granular surface. Processes tubular, open distally, approximately equal in length to radius of central body, terminating in a number of orthogonal or recurved spines.

HOLOTYPE. B.M.(N.H.) slide V.51741(1). 85 feet above base of London Clay ; Sheppey, Kent.

DIMENSIONS. Holotype : overall diameter 59 by 57 μ , diameter of central body 29 by 31 μ , length of processes 14–18 μ , width of processes up to 2 μ , number of processes 26.

DESCRIPTION. The processes are relatively thick walled, the tubule being narrow and sometimes constricted. At the bases of some of the processes there are small proximal elevations or swellings. Distally the processes splay out into 2 to 7 spines or secæ, up to 6 μ long. An apical archaeopyle is usually present. The tabulation reflected by the processes is that of *Hystrichosphaeridium*.

REMARKS. *H. sheppeyense* sp. nov. differs from *H. recurvatum* (White) in being considerably smaller and possessing relatively short processes. The forms described and figured by Deflandre & Cookson (1955) and by Evit (1961) are identical in all respects except that the former, from the Senonian, is rather larger. Deflandre & Cookson's figured specimen has an overall diameter of 90 μ , central body diameter of 44 by 51 μ and processes 16–26 μ in length.

***Hystrichosphaeridium bowerbanki* sp. nov.**

Pl. 8, figs. 1, 4

DERIVATION OF NAME. After J. S. Bowerbank who was one of the first British microscopists to record hystrichospheres from the Chalk, and the first to record them from the Upper Greensand.

DIAGNOSIS. Ovoidal to elongate central body with smooth surface. Processes thin-walled, tubular, open distally, sometimes widening considerably at their base, and greater than half the central body diameter in length. They terminate in a number of orthogonal or recurved spines. Apical archaeopyle usually present.

HOLOTYPE. Geol. Surv. Colln. slide PF.3033(1). Lower Chalk, H.M. Geological Survey Borehole, Fetcham Mill, Surrey at 730 feet depth. Upper Cretaceous (Cenomanian).

DIMENSIONS. Holotype : overall diameter 85 by 78 μ , diameter of central body 39 by 29 μ , length of processes 24–26 μ , number of processes 24. Range : overall diameter 60–85 μ , diameter of central body 29–40 μ , length of processes 21–26. Number of specimens measured, 5.

DESCRIPTION. The central body is characteristically ovoidal to elongate. The tubular processes are thin-walled and usually curved or bent to some extent. The distal spines are 5 to 7 in number and are up to 6 μ in length. The processes are cylindrical for most of their length, 2.5 to 3 μ wide and expand slightly distally to about 4 μ before giving rise to spines. Proximally the processes sometimes widen

considerably and may measure up to 10μ at their contact with the central body and often show noticeable basal wrinkles. An apical archaeopyle always appears to be present. The tabulation reflected by the processes is : (4'), 6", 6c, 5''', 1p, 1'''' and about 5s.

REMARKS. *H. bowerbanki* sp. nov. differs from *H. recurvatum* (White) in being smaller and having wider tubular processes. It is rather similar to *H. sheppeyense* but the form of the central body is more elongate ; the processes are wider, especially at their base, and have a much thinner wall.

OTHER SPECIES

The following species are here attributed to the genus *Hystrichosphaeridium* emend. on the basis of the number of processes and general form :

Hystrichosphaeridium cf. *clavigerum* (Deflandre) ; Lejeune-Carpentier 1940. Upper Cretaceous ; Belgium.

Hystrichosphaeridium irregulare (Merrill 1895). Lower Cretaceous ; U.S.A.

Hystrichosphaeridium stellatum (Maier 1959). Oligocene ; Germany.

The following described species are doubtfully included in *Hystrichosphaeridium* emend. on the basis of the number and form of processes present :

?*Hystrichosphaeridium arundum* (Eisenack & Cookson 1960). Upper Cretaceous ; Australia.

?*Hystrichosphaeridium aquitanicum* (Deunff 1961). Lower–Upper Cretaceous ; France.

?*Hystrichosphaeridium gliwicense* (Macko 1957). Miocene ; Poland.

?*Hystrichosphaeridium hilli* (Merrill 1895). Lower Cretaceous ; U.S.A.

?*Hystrichosphaeridium polyplasion* (Maier 1959). Miocene ; Germany.

Hystrichosphaeridium claviferum (Wilkinson 1849) ; Deflandre 1946a (incorrectly transferred to *Baltisphaeridium* by Downie & Sarjeant 1963) and *Hystrichosphaeridium cruciatum* O. Wetzel 1933 from the description and figures both appear to be the detached apical regions of species of *Hystrichosphaeridium* emend., bearing four processes. The holotype of *H. clavigerum* is lost ; it appears likely that it represents the apical region of *H. tubiferum*, of which the species *H. clavigerum* may be regarded as a junior synonym and should therefore be rejected. *H. cruciatum*, as illustrated by Lejeune-Carpentier (1940, fig. 14), represents the apical region of an otherwise undescribed species.

Genus **OLIGOSPHAERIDIUM** nov.

DERIVATION OF NAME. Greek, *oligo*, few or scanty ; *sphaera*, ball—with reference to the ball-like central body bearing a small number of processes.

DIAGNOSIS. Subspherical chorate cysts possessing a reflected tabulation of 4', 6", 5-6''', 1p, 1'''. Processes tubiform, open distally, intratabular, one process per plate area. Number of processes never more than 18. Archaeopyle apical.

TYPE SPECIES. *Xanthidium tubiferum complex* White 1842. Upper Cretaceous ; England.

REMARKS. Cingular processes are absent, there commonly being 6 postcingular processes. The processes are approximately of equal length on an individual but are variable within a species. They are always open and can be cylindrical to infundibular with perforate or entire walls. Endophragm confined to the central body, surrounded by periphragm which alone forms the processes. Processes never in contact with the interior of the central body.

An alternative formula for the reflected tabulation is : 4', 6", 5''', 1p, 1'''' and 0-1s. In the specimens possessing 14 processes, all are of the same size and one would expect if one sulcal process was present that this would be smaller than the other processes. This corresponds to the typical *Gonyaulax*-tabulation in which there are 6 postcingular plates, plate 1''' sometimes being considerably reduced. The original tabulation is tentatively reconstructed in Text-fig. 1.

Oligosphaeridium complex (White)

Pl. 7, figs. 1, 2 ; Pl. 10, fig. 3 ; Text-fig. 14

- 1842. *Xanthidium tubiferum complex* White : 39, pl. 4, div. 3, fig. 11.
- 1844. *Xanthidium tubiferum complex* White ; White : pl. 8, fig. 10 ; text-figs.
- 1848. *Xanthidium complexum* (White) Bronn : 1375.
- 1940. *Hystrichosphaeridium elegantulum* Lejeune-Carpentier : 22, text-figs. 11, 12.
- 1946. *Hystrichosphaeridium complex* (White) Deflandre : 11.
- 1952. *Hystrichosphaeridium complex* (White) ; Firtion : 156, pl. 9, figs. 2, 4, 5 ; text-fig. 1A-F.
- 1955. *Hystrichosphaeridium complex* (White) ; Deflandre & Cookson : 270, pl. 1, figs. 9, 10.
- 1955. *Hystrichosphaeridium complex* (White) ; Valensi : 592, pl. 4, fig. 3.
- ?1958. *Hystrichosphaeridium complex* (White) ; Cookson & Eisenack : 42, pl. 12, fig. 10.
- 1958. *Hystrichosphaeridium complex* (White) ; Eisenack : 400 pl. 26, 400, figs. 3-5 ; pl. 25, fig. 16?
- 1959. *Hystrichosphaeridium complex* (White) ; Gocht : 66, pl. 3, figs. 2, 3 ; pl. 7, figs. 5, 6.
- ?1962. *Hystrichosphaeridium tubiferum* (Ehr.) ; Pocock : 83, pl. 15, fig. 230.
- ?1963. *Hystrichosphaeridium tubiferum* (Ehr.) ; Baltes, pl. 2, figs. 1-3, 5, 6.
- 1964. *Hystrichosphaeridium complex* (White) ; Cookson & Hughes : 46, pl. 9, fig. 6.

EMENDED DIAGNOSIS. Central body sub-spherical to ovoidal. Wall composed of thin endophragm and periphragm, the latter giving rise to processes. Processes simple or branched, cylindrical for most of their length, open and expanded distally with aculeate or secate margin. Reflected tabulation inferred 4', 6", 5-6''', 1p, 1'''. Apical archaeopyle usually present having zig-zag margin. Processes in complete specimen not exceeding 18.

NEOTYPE. Geol. Surv. Colln. slide PF.3034(1). Lower Chalk, H.M. Geological Survey Borehole, Fetcham Mill, Surrey, at 750 feet depth. Upper Cretaceous (Cenomanian).

DIMENSIONS. Neotype : diameter of central body 35 by 35 μ , length of processes 22–25 μ . Range : diameter of central body 34–55 μ , length of processes 22–43 μ . Number of specimens measured, 9.

DESCRIPTION. In the specimens from the Cenomanian, the periphragm of the central body is smooth or very slightly granular. The processes are cylindrical for most of their length, with an expanded opening distally, the margin of which is developed into aculei and secae. The aculei and secae can be simple or branched, erect or patulate, orthogonal or even recurved. Where the processes meet the central body there is often a clearly marked ring indicating the point of divergence of the endophragm and periphragm. The wall of the processes is smooth or faintly fibrous ; their length usually measures between the radius and the diameter of the central body.

The small number of processes and the apical archaeopyle, when present, enable one readily to determine the tabulation of *O. complex* as reflected by the position of the processes.

Specimens of *O. complex* have been examined from two other horizons.

Examples from the Speeton Clay (Barremian) of Yorkshire are very similar to the forms illustrated by Eisenack (1958). The periphragm of the central body is often slightly granular and some of the processes are more deeply divided and show more variation than is usual in this species. 11 specimens were measured, the diameter of the central body being 35–62 μ and the length of the processes 13–47 μ .

Specimens from the London Clay (Ypresian) strongly resemble the Cenomanian forms, the processes perhaps being a little stouter. Diameter of central body 29–58 μ , length of processes 23–39 μ (6 specimens measured).

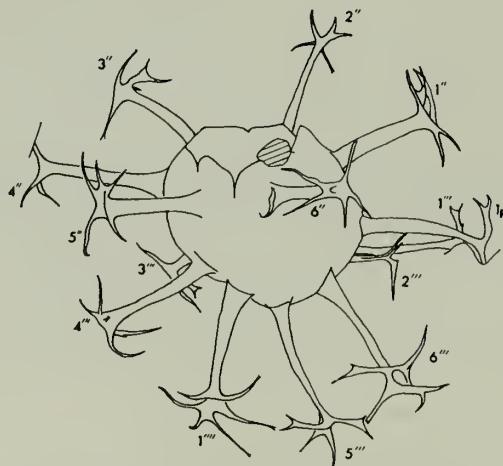


FIG. 14. *Oligosphaeridium complex* (White). A specimen from the Cenomanian, in lateral view, showing the angular apical archaeopyle and the distribution of the processes.
× c. 420.

O. complex thus has a stratigraphic range from the Neocomian (Gocht 1959 and Cookson & Eisenack 1958) to the Ypresian.

REMARKS. *Oligosphaeridium complex* was first described by White (1842) as *Xanthidium tubiferum complex*. In the description of the processes White stated : " Sometimes the orifice is separated into unequal divisions of four, five and six parts, in others like one variety of *X. ramosum* before noticed ; the branching terminations are of a more complex structure, each branch having at its extremes a further ramification ; at which last I am inclined not to consider a variety of one species, but the same as the former, in an advanced state of development. " Lejeune-Carpentier (1940) briefly described forms having distal prolongations under *Hystri-chosphaeridium elegantulum*. These she compared to *X. tubiferum complex* (White) and concluded that they were identical. In White's figures branching is clearly shown ; Lejeune-Carpentier's figures 11 and 12, however, suggest that some at least of the so-called distal branchings of the processes are bifurcating secæ of simple processes. *H. elegantulum* was transferred to *H. complex* by Deflandre (1946) on the grounds that it was an invalid synonym, but no new diagnosis was given for *H. complex*. Firtion (1952) figured different process terminations for the species. These cannot be seen in his indistinct plates and in his description he simply states " . . . the shell is furnished with tubiform radiating appendages ; their distal extremity very splayed-out, showing a system of fine and deep dentations. "

H. tubiferum (Cookson 1953, pl. 2, fig. 24) later placed in *H. complex* (Deflandre & Cookson 1955) is of doubtful status.

Valensi (1955) figured *H. complex*, branching in at least four processes. In the same year, Deflandre & Cookson enlarged the concept of this species by including within it specimens having cathrate extremities, transitional to *H. pulcherrimum*. Their figures closely approach the London Clay forms. Cookson & Eisenack (1958) figured *H. complex* with simple processes developed distally into aculei. Eisenack (1958) Gocht (1959) and Cookson & Hughes (1964) figured specimens with simple unbranched processes, produced distally into aculei.

Neale & Sarjeant (1962) in discussing their new species *H. macrotubulum* decided that forms possessing unbranched processes did not belong to *H. complex*. Partly on this basis, partly on the granular nature of the central body, they separated *H. macrotubulum* as a distinct species. In view of the uncertainty concerning the degree of branching of the processes, both branched and simple forms have been included in *H. complex*.

Much more significant is the tabulation inferred from the positions of the processes. The specimens of *H. complex* illustrated by Firtion (1952), Deflandre & Cookson (1955), Cookson & Eisenack (1958) and Gocht (1959) are clearly forms lacking cingulum processes and possessing an apical archaeopyle.

As Deflandre & Cookson (1955) noted, transitional forms to *H. pulcherrimum* occur, which have perforate processes ; the perforations are not, however, excessively numerous and for this reason the specimens concerned were placed in *H. complex*. Comparable forms have been observed in the Cenomanian of England.

The specimens attributed to *H. complex* by Baltes (1963, pl. 3, figs. 1–3) do not belong in this species. In contrast, the forms he illustrates as *H. tubiferum* (pl. 2, figs. 1–3, 5, 6) undoubtedly belong to *Oligosphaeridium* and probably to *O. complex*.

The holotype of *O. complex* from the British Senonian illustrated by White (1842, pl. 4, div. 3, fig. 11) cannot be traced. A neotype has therefore been chosen from the Cenomanian of Surrey (England).

***Oligosphaeridium reticulatum* sp. nov.**

Pl. 7, fig. 10

DERIVATION OF NAME. Latin, *reticulatus*, net-like—with reference to the reticulate or net-like appearance of the surface of the central body.

DIAGNOSIS. Subspherical central body composed of reticulate endophragm. Periphragm confined to processes, smooth or slightly fibrous. Processes simple, cylindrical, expanding distally and terminating in complicated aculeate or secate margin. Archaeopyle apical. Number of processes in complete specimen never exceeding 18. Inferred tabulation 4', 6", 5''', 1p, 1''' and 0–1s.

HOLOTYPE. Geol. Surv. Colln. slide PF.3035(1). Lower Chalk, Geological Survey Borehole, Fetcham Mill, Surrey, at 840 feet depth. Upper Cretaceous (Cenomanian).

DIMENSIONS. Holotype : diameter of central body 29 by 30 μ , length of processes 15–26 μ , number of processes 14. Range : diameter of central body 29–47 μ , length of processes 14–26 μ . Number of specimens measured, 5.

DESCRIPTION. The reticulate endophragm appears to be granular at low magnification, but at high magnification it is clearly seen to be finely reticulate. The cylindrical processes expand slightly proximally, forming a characteristic circle or oval on the surface of the central body. Distally they expand in the form of an open funnel often having an extremely ragged margin.

REMARKS. *O. reticulatum* sp. nov. is very similar to *O. complex*, differing only in the reticulate nature of the central body and the relative shortness of the processes. It is very significant that the inferred tabulations are identical, indicating a close phylogenetic relationship.

***Oligosphaeridium vasiformum* (Neale & Sarjeant)**

Pl. 9, fig 7 ; Pl. 10, fig. 1 ; Text-fig. 1

1962. *Hystrichosphaeridium vasiformum* Neale & Sarjeant : 452, pl. 20, fig. 1 ; text-fig. 8b.
1965. *Hystrichosphaeridium vasiformum* Neale & Sarjeant ; Sarjeant, text-fig. 3C.

EMENDED DIAGNOSIS. Sub-spherical to sub-quadrate central body composed of thin, smooth endophragm and thicker pitted periphragm. Not more than 18 processes present, composed of smooth periphragm. Processes simple, tubiform and expanding distally, distal margin bearing few spines.

HOLOTYPE. B.M.(N.H.) slide V.51709(1). Speeton Clay, Shell West Heslerton Borehole No. 1, Yorkshire, at 99.25 metres depth. Lower Cretaceous (Middle Hauterivian).

DIMENSIONS. Holotype : overall length 107.5μ , breadth 116μ , central body length 46.5μ (apical region lacking), breadth 52μ .

PARATYPE. B.M.(N.H.) slide V.51709(3) : overall length 124.5μ breadth 116μ , central body length 46.5μ (apical region lacking), breadth 46.5μ . Range ; overall lengths $107.5-130\mu$ (7 specimens).

DESCRIPTION. The periphragm on the surface of the central body is moderately thick and pitted to a varying extent. The pits, passing through the periphragm and exposing the endophragm, vary greatly in size, being as much as 1μ across. The processes arise from root-like bases and terminate distally in 4-6 simple spines. The processes do not connect with the interior of the central body. Rarely the processes possess small, often rectangular, areas where the periphragm is extremely thin, formerly described as perforations of the processes.

An apical archaeopyle is usually present, the resulting specimens possessing 14 processes. The inferred reflected tabulation is typical of the genus.

The species has only been recorded from the Middle Hauterivian.

REMARKS. *O. vasiiformum* is very similar to *O. complex* from the Barremian and is clearly related to it. The most important distinguishing features is the presence of the pitted periphragm on the surface of the central body in *O. vasiiformum*. The original tabulation of this species is tentatively reconstructed in Text-fig. 1.

O. reticulatum sp. nov. is another related form, but its processes are usually noticeably shorter and stouter with a much more complex distal margin.

***Oligosphaeridium macrotubulum* (Neale & Sarjeant)**

Pl. 9, fig. 4

1962. *Hystrichosphaeridium macrotubulum* Neale & Sarjeant : 452, pl. 20, fig. 7 ; text-fig. 8a.

REMARKS. A re-examination of the holotype has shown that the periphragm of the central body is pitted in exactly the same manner as in *O. vasiiformum*, albeit to a lesser extent. The processes have basically the same structure as in the latter species, but are perhaps slightly stouter than is typical. The holotype does not possess an archaeopyle, there being 18 processes present, indicating the reflected tabulation typical of this genus. As only the holotype of *O. macrotubulum* was examined the range of variation cannot be ascertained, but it is probable that this species is synonymous with *O. vasiiformum*.

***Oligosphaeridium pulcherrimum* (Deflandre & Cookson)**

Pl. 10, fig. 9 ; Pl. 11, fig. 5

1955. *Hystrichosphaeridium pulcherrimum* Deflandre & Cookson : 270, pl. 1, fig. 8 text-figs, 21, 22.

1955. *Hystrichosphaeridium pulcherrimum* Deflandre & Cookson ; Valensi : 592, pl. 4, fig. 1.

MATERIAL (figured). B.M.(N.H.) slide V.51742(1). Metropolitan Water Board Borehole No. 11 at 63 feet depth, London Clay ; Enborne, Berkshire.

REMARKS. The processes of the London Clay specimens indicate a reflected tabulation of 4', 6'', 6''', 1p, 1'''''. The apical processes are relatively small and an apical archaeopyle is usually present. The fenestrate appearance of the processes in this species are extremely distinctive. The London Clay forms may be derived.

DIMENSIONS. London Clay forms : diameter of central body 30–48 μ , length of processes 17–40 μ . Number of specimens measured, 3.

Oligosphaeridium prolixispinosum sp. nov.

Pl. 8, figs. 2, 3

DERIVATION OF NAME. Latin, *prolixus*, stretched out long and *spina*, thorny—with reference to the filiform spines at the distal extremities of the processes.

DIAGNOSIS. Elongate central body bearing few open tubular processes. Processes terminating distally in a number of long thread-like spines.

HOLOTYPE. Geol. Surv. Colln. slide PF.3036(1). Lower Chalk, H.M. Geological Survey Borehole, Fetcham Mill, Surrey, at 840 feet depth. Upper Cretaceous (Cenomanian).

DIMENSIONS. Holotype: overall width 64 μ , diameter of central body 40 by 20 μ , length of processes 18–24 μ , number of processes 17. Range : Length of central body, 33–43 μ , width 20–29 μ , length of processes 18–29 μ . Number of specimens measured, 8.

DESCRIPTION. The periphragm of the central body and of the processes is smooth. The processes are thin-walled and have a fairly broad base up to 8 μ , with characteristic basal wrinkles. There are noticeable circles beneath the processes where only endophragm is present. The processes are about 3 μ in width for most of their length tapering to 2 μ distally before giving rise to the filiform spines. The spines are extremely delicate, 5 to 8 in number, and up to 15 μ in length. The number of processes varies from 16 to 18, the variation probably due to the number of sulcal processes present. In all specimens there is an obvious apical archaeopyle. Surrounding the archaeopyle are 6 precingular processes, then a diastema before the postcingular processes are reached. This diastema marks the position of the cingulum. The processes on the hypotract are difficult to assign to any dinoflagellate tabulation. There is no obvious antapical process, in fact 3 antapical processes usually seem to be present. The reflected tabulation appears to be (4'), 6'', 6''', 3'''' and 1–3s.

O. prolixispinosum sp. nov. is a rare species occurring throughout the Cenomanian of Surrey.

REMARKS. *O. prolaxispinosum* sp. nov. is easily distinguishable from other species by its elongate form and small number of processes with very characteristic distal terminations. It should be noted that the basal wrinkles recorded in this species have also been seen in *Hystriosphæridium bowerbanki*.

At the base of the Cenomanian there have been found, together with normal examples of *O. prolaxispinosum*, two specimens, which possess exactly the same elongate central body and type of processes but there are present 22 and 25 processes. This unusual number is caused by the presence of 6 cingular processes. It would thus appear that *O. prolaxispinosum* is, in the Lower Cenomanian, rather an unstable species and not until later in the Cenomanian does it settle down, the cingular processes being absent.

Because of the above variation this species is rather difficult to classify since although the cingular processes are absent, it seems to be related to, or maybe even evolved from, a type possessing these processes. Two other factors are that the processes strongly resemble those found in *H. bowerbanki* and there may be 3 antapical processes present although this is uncertain. Until further information is available this species has been tentatively placed in the genus *Oligosphaeridium* because of the absence of cingular processes.

OTHER SPECIES

The following species are here attributed to the genus *Oligosphaeridium* on the basis of the number of processes and general form:

Oligosphaeridium albertense (Pocock 1962). Lower Cretaceous ; Canada.

Oligosphaeridium anthophorum (Cookson & Eisenack 1958). Upper Jurassic ; Australia and Papua.

Oligosphaeridium perforatum (Gocht 1959). Lower Cretaceous ; Germany.

Oligosphaeridium reniforme (Tasch, McClure & Oftedahl 1964). Lower Cretaceous ; U.S.A.

The following described species are doubtfully included in *Oligosphaeridium* on the basis of the number and form of the processes:

?*Oligosphaeridium asterigerum* (Gocht 1959). Lower Cretaceous ; Germany.

?*Oligosphaeridium coelenteratum* (Tasch, McClure & Oftedahl 1964). Lower Cretaceous ; U.S.A.

?*Oligosphaeridium dictyophorum* (Cookson & Eisenack 1958). Upper Jurassic ; Papua.

?*Oligosphaeridium dispare* (Tasch, McClure & Oftedahl 1964). Lower Cretaceous ; U.S.A.

?*Oligosphaeridium irregulare* (Pocock 1963 ; non Merrill 1895). Lower Cretaceous ; Canada.

?*Oligosphaeridium paradoxum* (Brosius 1963). Oligocene ; Germany.

Genus *PERISSEIASPHAERIDIUM* nov.

DERIVATION OF NAME. Greek, *perisseia*, abundance or surplus; *sphaera*, ball—with reference to the rather superfluous sulcal and cingular processes.

DIAGNOSIS. Chorate cysts with sub-spherical central body composed of two membranes. Processes of two types: (i) larger, tubiform, open distally and intratabular; one process per plate area, and (ii) smaller, closed processes restricted to sulcal and cingular regions. Tabulation reflected by tubiform processes 4', 6'', 5''', 1p, 1'''''. Archaeopyle apical.

TYPE SPECIES. *Perisseiasphaeridium pannosum* sp. nov.

REMARKS. This genus appears to be intermediate between *Hystrichosphaeridium* and *Oligosphaeridium*. It resembles the former in possessing both cingular and sulcal processes, but these are closed, and the latter since the tabular processes reflect a similar tabulation. It resembles *Hystrichokolpoma* in the presence of both tabular and closed processes, but the former are of a completely different type, being conical and covering most of the plate area. Also only 4 tabular postcingular processes are present in the genus *Hystrichokolpoma* whereas 5 are present in *Perisseiasphaeridium*.

Perisseiasphaeridium pannosum sp. nov.

Pl. 3, fig. 5; Pl. II, fig. 8; Text-fig. 15

DERIVATION OF NAME. Latin, *pannosus* ragged—with reference to the ragged or torn appearance of the infundibular processes.



FIG. 15. *Perisseiasphaeridium pannosum* sp. nov. A specimen from the London Clay, ventral view, showing the distribution of the processes. $\times$ c. 1000.

DIAGNOSIS. Chorate, sub-spherical to ovoidal cyst bearing two types of processes. One with broad open infundibular processes, often fenestrate distally ; the other with smaller slender processes, closed, with simple or bifurcate extremities. Apical archaeopyle present.

HOLOTYPE. B.M.(N.H.) slide V.51743(1). 155 feet above base of London Clay ; Whitecliff Bay, Isle of Wight.

DIMENSIONS. Holotype : diameter of central body 42.5 by 43μ ; length of infundibular processes $24-29\mu$; length of slender processes up to 19μ . Range : diameter of central body $42-57\mu$; length of infundibular processes $24-40\mu$; width of infundibular processes up to 9μ proximally, 34μ distally ; length of slender processes up to 27μ ; number of specimens measured, 4.

DESCRIPTION. This species has very distinctive infundibular processes with an irregular digitate margin, each branch being further split up into evexate, bulbous or bifid secæ. The secæ and/or the digitæ may be inter-connected, thus giving rise to a fenestrate structure. The tabulation reflected by the infundibular processes is $4'$, $6''$, $5'''$, $1p$, $1''''$. In addition there are some very slender processes, less than 1μ wide, restricted to the cingulum and sulcal zones. These processes are always closed, and are either acuminate or irregularly bifurcate. The exact number is variable and difficult to determine.

P. pannosum has only been recorded from the Ypresian of Britain.

REMARKS. This species differs from *Oligosphaeridium pulcherrimum* (Deflandre & Cookson) from the Australian Lower Cretaceous, in the nature of the fenestrate, infundibular processes. The slender cingular and sulcal processes are a characteristic feature.

OTHER SPECIES

Perisseiasphaeridium eisenacki sp. nov. The specimens described and figured by Eisenack (1958 : 402, pl. 26, figs. 1, 2) as *Hystriosphæridium anthophorum* Cookson & Eisenack from the Lower Cretaceous of Germany are here considered to belong to the genus *Perisseiasphaeridium* nov. and have been renamed accordingly.

Evitt (1961) pointed out that Eisenack's specimens possess definite fine cingular processes whereas the type material from the Upper Jurassic of Australia and Papua has a barren cingular zone and has been attributed to the genus *Oligosphaeridium* (see p. 77).

Genus *LITOSPHAERIDIUM* nov.

DERIVATION OF NAME. Greek, *litos*, plain or simple ; *sphaera*, ball—with reference to the simple arrangement of the processes on the surface of the central body.

DIAGNOSIS. Chorate cysts with spherical to sub-spherical central body composed of two membranes. Processes few in number (only one per plate area), hollow and open distally except for sulcal processes which may be closed. Reflected tabulation $3'$, $6''$, $5'''$, $1p$, $1''''$, with variable number of sulcal processes. Archaeopyle apical.

TYPE SPECIES. *Hystrichosphaeridium siphoniphorum* Cookson & Eisenack 1958. Probably Lower Cretaceous (Albian) ; Australia.

REMARKS. The presence of three apical processes and the absence of cingular processes is diagnostic of this genus, and makes it easily recognizable. The sulcal processes may be either absent or few.

***Litosphaeridium siphoniphorum* (Cookson & Eisenack)**

Pl. 7, figs. 7, 8 ; Text-figs. 16, 17

1958. *Hystrichosphaeridium siphoniphorum* Cookson & Eisenack : 44, pl. 11, figs. 8-10.

1963. *Hystrichokolpoma* sp. B., Baltes : 587, pl. 6, figs. 6-8.

1963. *Hystrichokolpoma* sp. A., Baltes : 587, pl. 6, figs. 1-5.

1964. *Hystrichosphaeridium siphoniphorum* Cookson & Eisenack ; Cookson & Hughes : 48, pl. 9, fig. 15.

EMENDED DIAGNOSIS. Spherical to sub-spherical central body composed of thin endophragm and thick reticulate periphragm. Processes, composed of smooth periphragm, varying considerably in shape and size but commonly cylindrical or sub-conical and always hollow. Distal margin of processes entire or serrate. Hexagonal apical archaeopyle usually present. Number of processes 13, rarely 14 or 15, in specimen possessing an archaeopyle. Inferred tabulation 3', 6'', 5''', 1p, 1'''' and 0-2s.

HOLOTYPE. National Museum of Victoria, Australia, specimen no. P17468, from Gingin Area, W.A., Seismic shot hole B2 at 230 ft. Horizon—probably Albian.

DIMENSIONS. Holotype : overall diameter 76 μ , diameter of central body 43 μ , length of processes c. 19-24 μ . Paratype : overall diameter 69 μ , diameter of central body 33 μ , length of processes c. 14 μ , operculum width 21 μ .

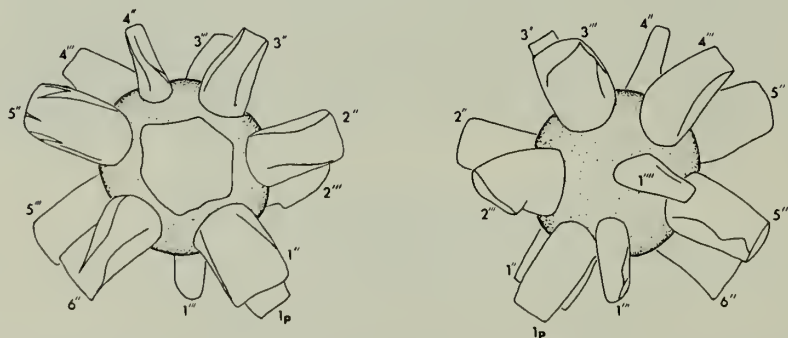


FIG. 16. *Litosphaeridium siphoniphorum* (Cookson & Eisenack). A specimen from the Cenomanian. Left, apical view, showing the six-sided archaeopyle and the arrangement of the processes ; right, antapical view. $\times$ c. 450.

Range of British Cenomanian forms : diameter of central body $21-47\mu$ (mean 34μ), length of processes $4-25\mu$. Number of specimens measured, 160.

DESCRIPTION. The periphragm of the central body at first sight appears to be granular, but at high magnification is seen to be reticulate. The processes, though normally cylindrical or subconical, can be mammiform or even saucer-shaped (Text-fig. 17), the latter being $4-5\mu$ in height. Very occasionally closed processes are present being either apical processes or small sulcal processes.

L. siphoniphorum has been recorded from the Albian of Australia and Roumania, and the Cenomanian of Australia and Britain.

REMARKS. The British Cenomanian specimens from Surrey agree fairly closely with the examples from Australia. The Surrey specimens appear to be smaller, but unfortunately the range of the Australian forms was not given in the description so no true size comparison can be made.

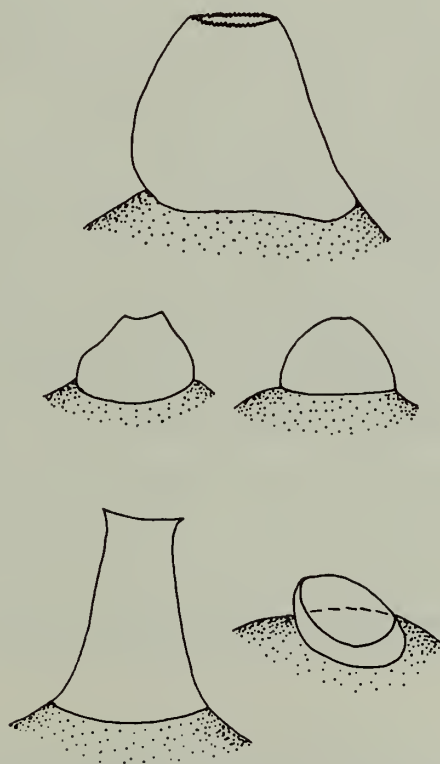


FIG. 17. *Litosphaeridium siphoniphorum* (Cookson & Eisenack). A figure illustrating the variation in the size and shape of the processes (based on specimens from the Cenomanian).

Baltes (1963) illustrated two forms (A and B) of this species from the Albian of Roumania. His species A has a central body diameter of $45-50\mu$ and species B one of approximately 25μ . In Britain it is interesting to note that the mean of the central body diameter (34μ) falls midway between these two forms. Thus it seems likely that *L. siphoniphorum* in Britain is represented in Roumania by two geographical subspecies, corresponding to Baltes' two forms, A and B.

?*Litosphaeridium inversibuccinum* sp. nov.

Pl. 12, fig. 3

DERIVATION OF NAME. Latin, *inversi*, inverted; *buccina*, trumpet—referring to the trumpet-like shape of the processes.

DIAGNOSIS. Sub-spherical or ovoidal central body, not exceeding 20μ in diameter, with sub-conical processes. Processes open distally, with denticulate or aculeate margin. Archaeopyle apical.

HOLOTYPE. B.M.(N.H.) slide V.51744(1). Metropolitan Water Board Borehole No. 11 at 83.25 feet depth, London Clay; Enborne, Berkshire.

DIMENSIONS. Holotype: diameter of central body 17 by 19μ , length of processes 7– 9μ , number of processes 13. Range: diameter of central body 11– 19μ , length of processes 4– 9μ . Number of specimens measured, 8.

DESCRIPTION. The wall of the central body is usually thin, but thick walled specimens have occasionally been encountered. The processes are not in connection with the interior of the central body and seldom exceed 15. The larger processes are sub-conical and may be up to 10μ wide at the base, rapidly decreasing in width to approximately $1.5-2\mu$, before expanding distally into a denticulate or aculeate margin. In addition to these stout processes there are usually one or two slender ones which are possibly closed distally. The latter are probably sulcal processes. An apical tetragonal archaeopyle was seen in one specimen, the archaeopyle being surrounded by 6 precingular processes. However the remaining tabulation is obscure.

REMARKS. ?*Litosphaeridium inversibuccinum* sp. nov. is easily distinguishable by its size and the form of its processes. It is tentatively placed in the genus *Litosphaeridium* because it possesses the correct number of processes to give the diagnostic tabulation of this genus, although the arrangement of the processes has, as yet, not been elucidated and a detached apical region has not been observed. The form of the processes and of the archaeopyle are both similar to those structures in *L. siphoniphorum*.

OTHER SPECIES

The following species are here tentatively referred to the genus *Litosphaeridium* on the basis of the number and type of processes:

?*Litosphaeridium crassipes* (Reade 1839). Upper Cretaceous ; England.

?*Litosphaeridium flosculus* (Deflandre 1937). Upper Cretaceous ; France.

?*Litosphaeridium truncigerum* (Deflandre 1937). Upper Cretaceous ; France.

Genus *CORDOSPHAERIDIUM* Eisenack 1963b : 261

EMENDED DIAGNOSIS. Sub-spherical chorate cysts, with central bodies composed of two distinct layers, periphragm variably developed, forming well developed processes, tubiform to buccinate, solid or hollow, intratabular and reflecting a tabulation of 1', 6'', 6c, 6''', (1p), 1'''' and a variable number of sulcal processes. Apical archaeopyle haplotabular never possessing zig-zag margin.

TYPE SPECIES. *Hystrichosphaeridium inodes* Klumpp 1953. Eocene ; Germany.

REMARKS. The genus *Cordosphaeridium* differs from related genera in the form of the archaeopyle. The archaeopyle has the shape of a convex triangle with rounded corners. At first sight it appears to be precingular but by study of the process arrangement it has been shown to be apical in position. It is formed by the loss of the single apical plate, the resulting archaeopyle being termed haplotabular (latin, *haplo*, single). The processes are usually strongly fibrous and can be either open or closed distally. There is little differentiation in the size of the processes, the cingulum processes being often, but not constantly, larger. The number of processes per plate within this genus varies considerably and it is probable that at a later date it will be necessary to sub-divide this genus taking this fact into account.

This genus was proposed by Eisenack (1963b) for forms possessing characteristically fibrous processes. Since it has been shown that hystrichospheres are cysts of dinoflagellates, the systematics of this group should be based on the tabulation reflected by the arrangement of the processes. It is therefore considered that the reflected tabulation is a better diagnostic feature than the fibrosity of the processes and the diagnosis has been emended accordingly. Other reasons against using the fibrosity of the processes as a generic distinction are that it is very variable within this genus and also that fibrous processes have been observed in other genera which have a distinct and different tabulation.

Cordosphaeridium inodes (Klumpp)

Pl. 3, fig. 9 ; Text-fig. 18

1953. *Hystrichosphaeridium truncigerum* Cookson : 114, pl. 2, figs. 21-23.

1953. *Hystrichosphaeridium inodes* Klumpp : 391, pl. 18, figs. 1, 2.

1955. *Hystrichosphaeridium inodes* Klumpp ; Deflandre & Cookson : 277, pl. 8, fig. 7.

1961. *Hystrichosphaeridium inodes* Klumpp ; Gerlach : 186, pl. 28, figs. 4-6.

1963. *Hystrichosphaeridium inodes* Klumpp ; Brosius : 40, pl. 5, fig. 5.

1963. *Cordosphaeridium inodes* (Klumpp) Eisenack : 261, pl. 29, fig. 3.

DESCRIPTION. *C. inodes* has a fibrous body wall, bearing processes which give the reflected tabulation typical of this genus. The variability in the number of processes, noticed by Klumpp, has also been observed in the London Clay forms, especially in the sulcal region. The processes are either hollow, open distally with an ellipsoidal cross-section or taeniate. The process walls of the London Clay specimens are extremely fibrous and appear to be thinner than in the type material, perhaps due to oxidation within the sediment.

C. inodes has been recorded from sediments ranging from the Lower Eocene to Middle Miocene in age.

MATERIAL (Figured). B.M.(N.H.) slide V.51745(I). 2 feet above base of London Clay ; Whitecliff, Isle of Wight.

DIMENSIONS. V.51745 : diameter of central body 46 by 48 μ , length of processes 19–24 μ . Range in type material (Klumpp 1953) : diameter of central body 52–76 μ , length of processes 20–40 μ . Range of London Clay forms : diameter of central body 46–76 μ , length of processes 14–33 μ . Number of specimens measured, 5.

***Cordosphaeridium gracilis* (Eisenack)**

Pl. 3, fig. 8 ; Pl. 11, figs. 4, 6, 7 ; Text-fig. 19

1938. *Hystrichosphaera* cf. *ramosa* (Ehr.) ; Eisenack : 186, text-fig. 1.

1954. *Hystrichosphaeridium inodes* subsp. *gracilis* Eisenack : 66, pl. 3, fig. 17 ; pl. 10, figs. 3–8 ; 112, figs. 7, 21.

1961. *Hystrichosphaeridium inodes* subsp. *gracilis* Eisenack ; Gerlach : 187, pl. 28, fig. 6.

1963b. *Cordosphaeridium inodes* subsp. *gracilis* (Eisenack) Eisenack, pl. 29, fig. 2.

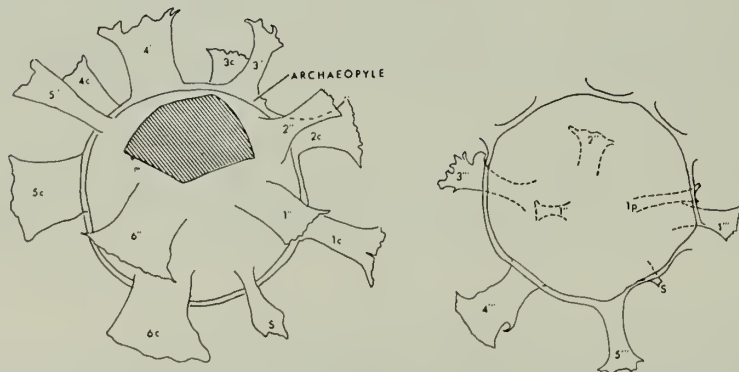


FIG. 18. *Cordosphaeridium inodes* (Klumpp). A specimen from the London Clay. Left, apical view ; right, antapical view, by transparency. $\times$ c. 650.

EMENDED DIAGNOSIS. Spherical to sub-spherical fibrous central body bearing small number of fibrous processes. Processes cylindrical, solid, erect, simple or branched and distinctly digitate ; intratabular, one per plate area, number never less than 19 or greater than 20. Archaeopyle apical, haplotabular, and reflected tabulation that of the genus *Cordosphaeridium*.

HOLOTYPE. Slide PH.10. Geologisch-Paläontologisches Institut der Universität Tübingen. Lower Oligocene ; Germany.

MATERIAL (figured). B.M.(N.H.) slide V.51746(1). 173 feet above base of London Clay ; Sheppey, Kent.

DIMENSIONS. Holotype : diameter of central body 77μ , overall diameter 166μ , length of processes $46\text{--}52\mu$. Range : diameter of central body $45\text{--}90\mu$, (mean 69μ), overall diameter $115\text{--}176\mu$. V.51746(1) : diameter of central body 64 by 69μ , length of processes $33\text{--}37\mu$. Range of London Clay specimens : diameter of central body $50\text{--}71\mu$, length of processes $20\text{--}43\mu$. Number of specimens measured, 12.

DESCRIPTION. The central body is characterized by a thick two-layered wall which is up to 2μ in thickness. The processes are strongly fibrous the fibres radiating outwards from the base of the processes over the surface of the central body, and when branched have a characteristic Y-shape. The single sulcal process is always included within the cingulum series.

REMARKS. This species was originally described and figured by Eisenack (1938c) as *Hystriosphæra* cf. *ramosa*. Eisenack (1954) proposed a sub-species of *Hystriosphæridium inodes* to include these forms on the basis of similar wall structure. The processes were described as solid, with fibrous branched endings, and the outer layer of the wall of the central body could be thicker than the inner one. The narrow hollow space in the interior of the processes at their base and passing through to the inner wall layer that Klumpp observed in *H. inodes* was not perceived with certainty by Eisenack for *H. inodes gracilis*. Eisenack (1954) noted and figured the

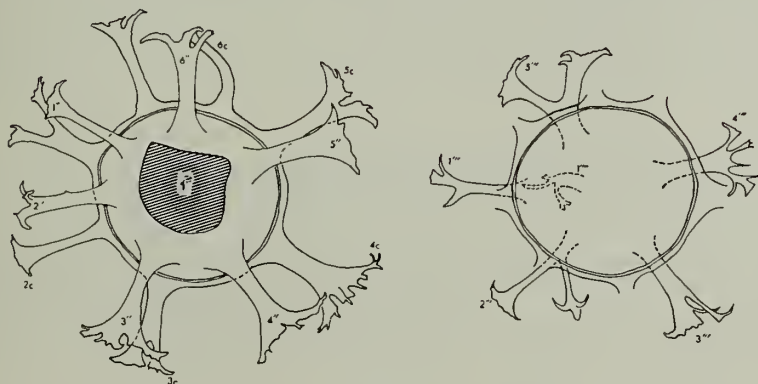


FIG. 19. *Cordosphaeridium gracilis* (Eisenack). A specimen from the London Clay. Left, apical view ; right, antapical view, by transparency. $\times$ c. 650.

archaeopyle and the operculum with a single process (plate 10, fig. 8). Gerlack (1961) similarly noticed a "pylome" in *H. inodes gracilis* (plate 28, fig. 6). In 1963, Eisenack transferred *H. inodes* and *H. inodes gracilis* to the new genus *Cordosphaeridium*.

Because of the observed differences to *C. inodes*, namely the variable thickness of the periphragm and endophragm, the absence of a narrow hollow space at the base of the processes, the solid structure and peculiar branching of the processes, it is felt that Eisenack's subspecies merits raising to the specific level.

All of Eisenack's findings are verified in the London Clay specimens. Apart from their larger size, Eisenack's and Gerlack's forms are identical with the London Clay examples.

Cordosphaeridium fibrospinosum sp. nov.

Pl. 5, fig. 5

DERIVATION OF NAME. Latin, *fibra*, fibrous; *spinosus*, thorny—with reference to the fibrous spines.

DIAGNOSIS. Ovoidal central body with wall up to 0.5μ thick, composed of smooth endophragm and fibrous periphragm. Processes fibrous, often very broad and ovoidal in cross-section, walls perforate. Processes open distally, with entire or undulose margin. One process per plate reflecting a tabulation typical of genus. Archaeopyle apical haplotabular.

HOLOTYPE. B.M.(N.H.) slide V.51747(1). Metropolitan Water Board Borehole No. 11 at 53 feet depth, London Clay; Enborne, Berkshire.

DIMENSIONS. Holotype: diameter of central body 63 by 67μ , length of processes 15 – 28μ , width of processes 5 – 25μ . Range: diameter of central body 59 – 72μ , length of processes up to 39μ , width of processes up to 26μ . Number of specimens measured, 5.

DESCRIPTION. This species is characterized by fibrous, often perforate, processes which can be latispinous. The perforations show no regularity in arrangement and tend to be elongate. The cross-section of the processes is ovoidal or rarely cylindrical and then only in the narrower processes. The lengths of the processes vary considerably in different specimens but rarely exceed half the diameter of the central body. It should be noted that in the broader processes, the width often exceeds the length.

C. fibrospinosum sp. nov. has been recorded throughout the London Clay of England.

REMARKS. The short, perforate processes, varying considerably in width but often very wide, make *C. fibrospinosum* an easily distinguishable species.

Cordosphaeridium cracenospinosum sp. nov.

Pl. 3, fig. 4

DERIVATION OF NAME. Latin, *cracens*, graceful or slender; *spinosus*, thorny—with reference to the appearance of the processes.

DIAGNOSIS. Sub-spherical to polygonal central body with wall composed of endophragm and periphragm, up to 1.5μ in thickness. Endophragm very thin. Archaeopyle apical haplotabular; processes slender, buccinate, erect, or curved, solid or with fine central tubule or hollow, the last two types open distally. Distal margins foliate, bifurcate or digitate. Processes one per plate area.

HOLOTYPE. B.M.(N.H.) slide V.51748(1). Metropolitan Water Board Borehole No. 39 at 170 feet depth, London Clay; Enborne, Berkshire.

DIMENSIONS. Holotype: diameter of central body 122 by 125μ , length of processes up to 66μ . Range: diameter of central body 75– 125μ , length of processes 17– 76μ . Number of specimens measured, 5.

DESCRIPTION. The large central body of *C. cracenospinosum* sp. nov. has a finely reticulate surface. In overall outline this species appears to be sub-spherical, but closer examination shows that often it tends to be polygonal. The processes are generally single, rarely branched, and in length often exceed half the diameter of the central body. The periphragm often forms a ridge on the surface of the central body where a process arises. Occasionally very fine, shorter processes are present. Many of the processes are solid, others having a narrow central cavity throughout their length or being hollow tubiform. Distally there is considerable variation, digitate endings being the commonest.

This species of *Cordosphaeridium* has been observed in samples throughout the London Clay of England.

REMARKS. *C. cracenospinosum* differs from *C. gracilis* by its thinner wall, which is only very faintly fibrous, the shape of the central body and the occasional presence of smaller, very fine, processes. It is unusual in having solid and hollow processes, the former however predominate. Process endings comparable to those in *Baltisphaeridium pectiniforme* Gerlack (1961) from the Oligocene of Germany, are occasionally encountered.

Cordosphaeridium exilimurum sp. nov.

Pl. 11, fig. 2

DERIVATION OF NAME. Latin, *exilis*, thin or meagre; *murus* wall—with reference to the rather thin wall of the central body.

DIAGNOSIS. Ovoidal central body, composed of thin, smooth or slightly granular endophragm with fine fibrils of periphragm running over surface. Processes tubiform or buccinate, of variable width, and rarely latispinous, distally open with serrate or undulose margin. Wall of processes thin and often fenestrate.

HOLOTYPE. B.M.(N.H.) slide V.51749(1). 275 feet above the base of London Clay ; Whitecliff Bay, Isle of Wight.

DIMENSIONS. Holotype : diameter of central body 44 by 54μ , length of processes 18–26 μ . Range : diameter of central body 44–98 μ , length of processes 16–42 μ . Number of specimens measured, 7.

DESCRIPTION. Haplotabular archaeopyle and tabulation characteristic of the genus *Cordosphaeridium*. The number of processes per plate area is one, but occasionally a fine subsidiary process may be present. Fine processes also occur in the sulcal region. Both the endophragm and periphragm are extremely thin, especially the latter when forming the processes. The wall of the processes is smooth or fibrous ; in the former the fibrils are only faintly developed. Whether or not the processes are always fenestrate is difficult to determine, even at high magnification, on account of the thinness of the periphragm. The processes rarely exceed half the diameter of the central body ; they are up to 10 μ wide meridionally and distally extremely expanded. Adjacent processes are occasionally united distally.

C. exilimurum has been recorded throughout the London Clay of England.

REMARKS. No other described species possesses fine, often perforate processes with an apical haplotabular archaeopyle and tabulation 1', 6'', 6c, 6''', 1'''' and a variable number of sulcal processes. ?*C. cantharellum* (Brosius 1963) is similar in general form but possesses stronger, more cylindrical processes which are never perforate or united distally, and often have a recurved distal margin.

Cordosphaeridium latispinosum sp. nov.

Pl. 5, fig. 8

DERIVATION OF NAME. Latin, *latus*, broad ; *spinosus*, thorny—with reference to the very wide processes present in this species.

DIAGNOSIS. Ellipsoidal central body having a finely striate periphragm from which arise two types of processes : broad ovoidal to quadrate ones, closed or with restricted distal opening, and slender oblate processes. Larger processes reflecting a tabulation of 1', 6'', 6''', 1'''' ; smaller ones restricted to sulcal and cingulum regions.

HOLOTYPE. B.M.(N.H.) slide V.51746(2). 173 feet above base of London Clay ; Sheppey, Kent.

DIMENSIONS. Holotype : diameter of central body 56 by 61 μ , length of processes up to 22 μ . Range : diameter of central body 50–77 μ , length of processes 11–24 μ , width of broad processes up to 27 μ . Number of specimens measured, 5.

DESCRIPTION. The broad processes of *Cordosphaeridium latispinosum* sp. nov. are quadrate or ellipsoidal in cross-section proximally. They taper distally and have a slightly fibrous wall which may be perforate with small lateral spines : the broad processes are found on the apical, pre- and postcingular, posterior intercalary and antapical plate areas. The slender processes appear to be sulcal or cingular processes.

They can be simple or bifurcate, distally they are oblate or acuminate. The striae on the periphragm radiate outwards from the bases of the processes over the surface of the central body.

C. latispinosum has been recorded from the London Clay of Sheppey, Kent and Enborne, Berkshire.

REMARKS. *C. latispinosum* differs from ?*Litosphaeridium truncigerum* Deflandre 1937 from the Upper Cretaceous of France, in the nature of the broad processes. In ?*L. truncigerum* these are widely open with denticulate margins, whereas in *C. latispinosum* they are closed or have a restricted elongate opening with lateral spines developed.

***Cordosphaeridium divergens* (Eisenack)**

Pl. 12, fig. 2

1938. *Hystrichosphaeridium* sp., Eisenack : 185, text-fig. 3.

1954. *Hystrichosphaeridium divergens* Eisenack : 67, pl. 9, figs. 13–16.

1963. *Baltisphaeridium divergens* (Eisenack) Downie & Sarjeant : 91.

1963b *Cordosphaeridium divergens* (Eisenack) Eisenack : 262, pl. 29, fig. 4.

DESCRIPTION. Specimens of *C. divergens* from the London Clay possess an apical haplotabular archaeopyle and the tabulation of the genus *Cordosphaeridium*. Eisenack (1954) noted and figured the archaeopyle and correctly indicated that the margin of it lay parallel to the equator. Specimens having a reticulate surface, as observed by Eisenack from the Oligocene, are also found in the London Clay. The processes are intratabular, there being at least 4 on each precingular area. In structure they compare favourably with those of the type material.

MATERIAL (Figured). B.M.(N.H.) slide V.51750(1). 157 feet above the base of London Clay ; Whitecliff, Isle of Wight.

DIMENSIONS. V.51750(1) : diameter of central body 45 by 47 μ , length of processes 14–22 μ . Range of London Clay forms : diameter of central body 38–52 μ , length of processes 12–21 μ . Number of specimens measured, 5.

REMARKS. *C. divergens* superficially resembles *Baltisphaeridium* cf. *intermedium* Deflandre (1938) from the Oxfordian, differing only in its slightly larger size. As yet species belonging to the genus *Cordosphaeridium* have not been recorded from horizons earlier than the Eocene.

***Cordosphaeridium multispinosum* sp. nov.**

Pl. 3, fig. 6

DERIVATION OF NAME. Latin, *multi*, many or numerous ; *spinosus*, thorny—with reference to the numerous processes.

DIAGNOSIS. Sub-spherical to ovoidal central body. Thin endophragm and fibrous periphragm giving rise to numerous, more than 45, short fibrous processes.

Processes taeniate, solid, undulose with serrate or digitate distal margins, sometimes arranged in meridional rows, sometimes haphazard in position.

HOLOTYPE. B.M.(N.H.) slide V.51751(1). 173 feet above base of London Clay ; Sheppey, Kent.

DIMENSIONS. Holotype : diameter of central body 56 by 59 μ , length of processes up to 15 μ . Range : diameter of central body 45–59 μ , length of processes up to 24 μ . Number of specimens measured, 4.

DESCRIPTION. The processes are numerous, generally simple with parallel edges expanding proximally and distally. Some of the processes are regularly linked proximally in such a manner as to give rise to six long rows, running from apex to antapex. Between these rows the arrangement of the other processes appears to be haphazard. There appear to be 2, rarely 3, processes per plate area. The maximum width of the processes is 7 μ , and their length one-quarter to one-third (rarely up to one-half) the diameter of the central body. Occasionally fine, acuminate processes are present on the central body. There is a well developed archaeopyle with an uninterrupted margin.

C. multispinosum sp. nov. has been recorded from the London Clay of Whitecliff Bay, Isle of Wight, Hampshire and the Isle of Sheppey, Kent.

REMARKS. In the linear arrangement of some of the processes and the haphazardous nature of others *C. multispinosum* differs from all other species of *Cordosphaeridium*.

?*Cordosphaeridium fasciatum* sp. nov.

Pl. 7, figs. 5, 6

DERIVATION OF NAME. Latin, *fasciatus*, striped—with reference to the striped appearance of the central body due to the thickenings of the periphragm.

DIAGNOSIS. Spherical to sub-spherical central body composed of reticulate endophragm of fibrous periphragm. Processes, composed of periphragm, smooth or slightly fibrous, short, wide and tubiform, always hollow and denticulate distally.

HOLOTYPE. B.M.(N.H.) slide V.51719(1). Speeton Clay, Shell West Heslerton Borehole No. 1, Yorkshire, at 42.5 metres depth. Lower Cretaceous (Lower Barremian).

DIMENSIONS. Holotype : diameter of central body 40 by 40 μ , length of processes 11–16 μ , number of processes 19. Range : diameter of central body 35–47 μ , length of processes 12–25 μ . Number of specimens measured, 6.

DESCRIPTION. From the base of each process, thickenings of the periphragm radiate over the surface of the central body joining together with similar thickenings from neighbouring processes. The reticulate nature of the endophragm can sometimes be observed where the periphragm thins midway between processes and also at the bases of the processes when one is able to view directly down the centre of a vertical process (Pl. 7, fig. 6). The processes have parallel or sub-parallel sides

throughout their length. There are 18 to 20 processes, an apical archaeopyle usually being present. The shape and form of the archaeopyle is difficult to determine and a detached apical region has not, as yet, been observed. However the archaeopyle is thought to be haplotabular and the spines to have an inferred reflected tabulation of 1', 6'', 6c, 5''', 1'''' and 0-2s.

?*C. fasciatum* sp. nov. has only been recorded from the Lower Barremian of Yorkshire.

REMARKS. The short, wide tabular processes differentiate this species from ?*C. eoinodes* (Eisenack) and the nature of the periphragm on the central body is probably different although this was not commented on in the original diagnosis or description. The nature of the periphragm on the surface of the central body and when composing the processes of *Hystrichosphaeridium radiculum* sp. nov. and *H. mantelli* sp. nov. is very similar to *C. fasciatum* perhaps indicating a relationship between the three species. Each form possesses a distinctive type of process and the two forms of *Hystrichosphaeridium* have a greater number of processes than does *C. fasciatum*. The type of archaeopyle is a very important factor in determining the above relationships but unfortunately the exact type of archaeopyle has not been determined as yet.

?*C. fasciatum* is thought to belong to *Cordosphaeridium* on account of the probable presence of a haplotabular archaeopyle, the number of processes and the fibrous nature of the periphragm so commonly observed in species of this genus.

OTHER SPECIES

The following species are here tentatively referred to the genus *Cordosphaeridium* Eisenack 1963, emend. on the basis of the number and type of processes:

?*Cordosphaeridium cantharellum* (Brosius 1963). Oligocene ; Germany.

?*Cordosphaeridium difficile* (Manum & Cookson 1964). Upper Cretaceous ; Arctic Canada.

?*Cordosphaeridium diktyoplokus* (Klumpp 1953). Eocene ; Germany.

?*Cordosphaeridium diktyoplokus* subsp. *latum* (Klumpp 1953). Eocene ; Germany.

?*Cordosphaeridium eoinodes* (Eisenack 1958). Lower Cretaceous ; Germany.

?*Cordosphaeridium erectum* (Manum & Cookson 1964). Upper Cretaceous ; Canada.

?*Cordosphaeridium floripes* (Deflandre & Cookson 1955). Miocene ; Australia.

?*Cordosphaeridium floripes* subsp. *breviradiatum* (Cookson & Eisenack 1961). Eocene ; Australia.

?*Cordosphaeridium microtriaina* (Klumpp 1953). Eocene ; Germany.

Genus **POLYSPHAERIDIUM** nov.

DERIVATION OF NAME. Greek, *polys*, many ; *sphaero*, ball—with reference to the central spherical body which bears numerous processes.

DIAGNOSIS. Chorata cysts possessing sub-spherical to ovoidal central body and bearing numerous processes all similar in size. Number of processes per plate area

greater than one, not normally more than four. Processes hollow, open or closed distally, process cavity not connecting with interior of central body. Archaeopyle, when present, apical with angular margin.

TYPE SPECIES. *Polysphaeridium subtilum* sp. nov. Eocene (Ypresian) ; England.

REMARKS. The processes are typically fairly short and expand distally, terminating by a serrate or spinous margin. The number of processes present makes it extremely difficult for the reflected tabulation to be determined, but is undoubtedly basically the same as that possessed by *Hystrichosphaeridium tubiferum* (Ehr).

As this genus now stands it contains a large number of species having in common an archaeopyle and a large number of hollow processes, but otherwise unrelated. At some future date, fuller knowledge of this genus will undoubtedly necessitate its subdivision, perhaps on the basis of process form.

***Polysphaeridium subtile* sp. nov.**

Pl. 11, fig. 1

DERIVATION OF NAME. Latin, *subtilus*, thin or slender—with reference to the slenderness of the processes.

DIAGNOSIS. Central body, sub-spherical to sub-rectangular, with wall composed of extremely thin smooth endophragm and thin granular periphragm. Processes not in connection with interior, slender, open distally, with serrate margin. Average length of processes, one-fifth to one-third the diameter of central body. Number of processes greater than 60.

HOLOTYPE. B.M.(N.H.) slide V.51752(1). 178 feet above base of London Clay; Sheppey, Kent.

DIMENSIONS. Holotype : diameter of central body 47–48 μ , length of processes 10–16 μ . Range : diameter of central body 31.5–50 μ , length of processes 6–16 μ . Number of specimens measured, 5.

DESCRIPTION. Simple, slender, tubiform processes possessing a usually serrate distal margin. The latter is occasionally entire, and may be circular or oval. The width of the processes never exceeds 2 μ . The processes do not appear to be arranged in any regular pattern.

REMARKS. *P. subtile* sp. nov. is distinguished from all other species by the number and form of the open processes present.

***Polysphaeridium pastielsi* sp. nov.**

Pl. 4, fig. 10

1948. *Hystrichosphaeridium pseudohystrichodinium* (Deflandre) ; Pastiels : 43, 3, figs. 12–15.

DERIVATION OF NAME. In honour of André Pastiels, who made pioneer studies in the Eocene microplankton of Belgium.

DIAGNOSIS. Ovoidal central body with smooth or granular surface. Apical archaeopyle with zig-zag margin. Processes numerous, all of one type; simple open, tapering distally to narrow neck before spreading slightly to an opening with entire or serrate margin. Processes sometimes united proximally, slightly fibrous.

HOLOTYPE. B.M.(N.H.) slide V.51753(1). 99 feet above base of London Clay; Sheppey, Kent.

DIMENSIONS. Holotype: diameter of central body $37-43\mu$, length of processes $10-14\mu$. Range: diameter of central body $31-43\mu$, length of processes up to 19μ . Number of specimens measured, 5.

DESCRIPTION. The processes broaden proximally, often quite considerably, and may measure up to 9μ in width but the latter is very variable. An apical archaeopyle is present.

REMARKS. The Ypresian forms illustrated by Pastiels (1948) as *Hystrichosphaeridium pseudohystrichodinium* strongly resemble the London Clay forms. The holotype of Deflandre has long supple processes, thinning regularly towards the extremity which is simple, or fluted, or with a very small fork. *P. pastielsi* is therefore a separate species which superficially resembles *H. pseudohystrichodinium*.

?*P. asperum* (Maier) is described as having an oval granular central body. The processes are open, tapering, terminating distally in 2-3 spines. This distal margin is not unlike the denticulate lip sometimes observed in *P. pastielsi*. The two species may even be conspecific.

P. simplex (White) as illustrated by Gerlach (1961) and by Brosius (1963) are both probably conspecific with *P. pastielsi*. They differ from White's holotype which possesses longer and fewer processes with greatly expanded distal openings.

***Polysphaeridium pumilum* sp. nov.**

Pl. 7, figs. 3, 4

?1955. *Hystrichosphaeridium recurvatum* (White); Deflandre & Cookson: 269, pl. 1, fig. 12.

DERIVATION OF NAME. Latin, *pumilus*, dwarfish or little—with reference to the small size of this species.

DIAGNOSIS. Subspherical central body having numerous small open tubular processes. Processes terminating distally in a slightly recurved more or less entire margin. Length of processes less than half that of the maximum body diameter.

HOLOTYPE. Geol. Surv. Colln. slide PF.3037(1). Lower Chalk, H.M. Geological Survey Borehole, Fetcham Mill, Surrey at 750 feet depth. Upper Cretaceous (Cenomanian).

DIMENSIONS. Holotype: overall diameter 40 by 34μ , diameter of central body 25 by 19μ , length of processes $8-10\mu$. Number of processes c.44. Range: overall diameter $30-40\mu$, diameter of central body $17-25\mu$, length of processes $7-10\mu$,

width of processes $1-1.5\mu$, number of processes 38-44. Number of specimens measured, 3.

DESCRIPTION. The central body has a smooth surface. The processes are tubular with a thin wall. They widen slightly both proximally, at the junction with the central body, and distally up to about 2μ . The distal termination of a process superficially strongly resembles that of *Hystrichosphaeridium sheppeyi* sp. nov., but on closer examination the presence of spines has not been observed. The distal margin is probably entire or slightly denticulate. The number of processes present indicate that each precingular and postcingular plate area bears two processes. An archaeopyle has not been observed with certainty.

REMARKS. This species is clearly differentiated from all other species by its size and the number and type of processes present. It appears to be very similar to Deflandre & Cookson's second series of specimens described as *Hystrichosphaeridium recurvatum* (White); however the Australian examples of Lower Cretaceous age seem to be larger, although the correct number of processes for the species is present. Deflandre & Cookson (1955, pl. 1, fig. 12) illustrate a specimen with seemingly similar processes to the British Cenomanian examples.

Polysphaeridium laminaspinosum sp. nov.

Pl. 8, fig. 8

DERIVATION OF NAME. Latin, *lamina*, blade; *spinosus*, thorny—referring to the flattened blade-like appearance of the processes.

DIAGNOSIS. Spherical to sub-spherical central body composed of reticulate endophragm. Processes numerous, approximately 36 in number, composed of periphragm; cylindrical, smooth and delicate, terminating in entire margin. Characteristic circular impression occurring where process arises from central body.

HOLOTYPE. Geol. Surv. Colln. slide PF.3052. Lower Chalk, H.M. Geological Survey Borehole, Fetcham Mill, Surrey, at 650 feet depth. Upper Cretaceous (Cenomanian).

DIMENSIONS. Holotype: diameter of central body 27 by 27μ , length of processes 11-15 μ , number of processes 36. Range; diameter of central body 23-28 μ , length of processes 11-17 μ . Number of specimens measured, 6.

DESCRIPTION. The endophragm appears to be granular until examined under high magnification when the reticulate nature becomes apparent. The processes are broadly tubular, up to 5μ in width, usually flattened and are often bent. A few of the processes are clearly truncated at their distal extremity, but most splay out slightly and have a corrugated entire margin. A 6-sided apical archaeopyle has been observed in one specimen. The number of processes present indicate that there are two per plate.

P. laminaspinosum is a rare species found throughout the Cenomanian of Fetcham Mill, Surrey.

REMARKS. The size, number and nature of the processes make it easy to distinguish *P. laminaspinosum* from all previously described species. The processes are longer and more distinctly tubular than is usual for this genus. If more species of this form are discovered a new genus should be erected to differentiate these types from the typical species of *Polysphaeridium*.

OTHER SPECIES

The following species are here tentatively referred to the genus *Polysphaeridium* on the basis of the form of the processes although an apical archaeopyle has not been recorded in any of them.

?*Polysphaeridium asperum* (Maier 1959). Miocene ; Germany.

?*Polysphaeridium deflandrei* (Valensi 1947). Middle Jurassic ; France.

?*Polysphaeridium* cf. *elegantulum* (Wiler 1956). Tertiary ; Germany.

?*Polysphaeridium fabium* (Tasch, McClure & Oftedahl 1964). Lower Cretaceous ; U.S.A.

?*Polysphaeridium fluctuans* (Pastiels 1948). Eocene ; France.

?*Polysphaeridium folium* (Tasch, McClure & Oftedahl 1964). Lower Cretaceous ; U.S.A.

?*Polysphaeridium fucosum* (Valensi 1955). Cretaceous ; France.

?*Polysphaeridium marsupium* (Tasch, McClure & Oftedahl 1964). Lower Cretaceous ; U.S.A.

?*Polysphaeridium major* (Lejeune-Carpentier 1940). Upper Cretaceous ; Belgium.

?*Polysphaeridium paulinae* (Valensi 1953). Middle Jurassic ; France.

?*Polysphaeridium perovatum* (Tasch, McClure & Oftedahl 1964). Lower Cretaceous ; U.S.A.

?*Polysphaeridium polytes* (= *H. recurvatum* subsp. *polytes* Cookson & Eisenack 1962). Lower-?Upper Cretaceous ; Australia.

?*Polysphaeridium rhabdophorum* (Valensi 1955). Cretaceous ; France.

?*Polysphaeridium simplex* (White 1842). Upper Cretaceous ; England.

?*Polysphaeridium tribrachiosum* (Tasch, McClure & Oftedahl 1964). Lower Cretaceous ; U.S.A.

?*Polysphaeridium zoharyi* (Rossignol 1962). Pleistocene ; Israel.

Genus **DIPHYES** Cookson 1965 : 85

EMENDED DIAGNOSIS. Chorates cysts with ovoidal to spherical central body composed of two layers. Processes numerous, 1 to 4 per plate area, hollow and either open or closed distally. Large antapical process occurring opposite apical archaeopyle.

TYPE SPECIES. *Hystrichosphaeridium colligerum* Deflandre & Cookson 1955. Eocene ; Australia.

REMARKS. The genus *Diphyes* is here restricted to include forms possessing two types of processes—numerous fine ones and a single large antapical. *D. nudum* Cookson does not possess any processes at all and certainly does not belong in this genus.

***Diphyes colligerum* (Deflandre & Cookson)**

Pl. 4, figs. 2, 3

1953. *Hystrichosphaeridium* sp. C. Cookson : 115, pl. 2, figs. 29, 30.
 1955. *Hystrichosphaeridium colligerum* Deflandre & Cookson : 278, pl. 7, fig. 3.
 1962. *Hystrichosphaeridium colligerum* Deflandre & Cookson ; Cookson & Eisenack : 44, pl. 2, fig. 9.
 1963. *Baltisphaeridium colligerum* (Deflandre & Cookson) Downie & Sarjeant : 91.
 1965. *Diphyes colligerum* (Deflandre & Cookson) Cookson : 86, pl. 9, figs. 1–12.

EMENDED DIAGNOSIS. Ovoidal to spherical central body with wall composed of thin endophragm and outer finely reticulate periphragm. Processes composed of periphragm, numerous, simple, hollow, open or closed distally. One single broad antapical process. Total number of processes exceeding 50.

HOLOTYPE. P.16301, National Museum of Victoria, Australia. Princetown Member of Dilwyn Clay, Lower Eocene ; Point Ronald, Vic. Dept. of Mines bore, Victoria.

MATERIAL (Figured). B.M.(N.H.) slide V.51754(1). 157 feet above base of London Clay ; Whitecliff Bay, Isle of Wight.

DIMENSIONS. Holotype : diameter of central body 33μ , overall diameter 56μ , length of antapical process 20μ , width of antapical process 13μ , length of small processes approx. 13μ . Range : diameter of central body 30 – 33μ , overall diameter 56 – 59μ , length of small processes approx. 13μ . Figured specimens diameter of central body 33 by 37.5μ , length of antapical process 16μ , width of antapical process 15μ , length of small processes 11 – 15μ . Range of English specimens : diameter of central body 29 – 41μ , length of antapical process 16 – 21μ , width of antapical process 8 – 15μ , length of small processes 8 – 15μ .

DESCRIPTION. An apical archaeopyle and the large antapical process enable easy orientation of specimens of this species. The antapical process is hollow, cylindro-conical, occasionally closed, and bears small tubules, 2 – 3μ long, towards the distal extremity. The tubules can take the form of simple conical protuberances or can have slightly bifurcate extremities. The smaller processes are commonly simple, occasionally united proximally, and may be open or closed distally. They are slender but do vary in width, and in specimens possessing open processes they taper to a distal neck before terminating with a slightly expanded opening. The distal margin may be finely serrate or entire. Both types of processes are slightly fibrous and do not communicate with the interior of the central body. There are commonly 4, regularly distributed, processes for each precingular plate area ; 2 – 4 for the postcingular plate areas and a constant 2 in the cingular plate areas.

REMARKS. The diagnosis of *Diphyes* has been emended to relate the process arrangement to a dinoflagellate tabulation, and to draw attention to the single antapical process.

In the original diagnosis, the smaller processes are said to be closed. The figure by Deflandre & Cookson (1955, pl. 7, fig. 3) seems to indicate, however, that the processes are open, as in the examples from the London Clay. Cookson & Eisenack (1961, pl. 2, fig. 9) figured *H. colligerum* with the processes definitely open. The species may well be confined to examples with open processes after re-examination of the holotype. Cookson (1965, pl. 9, figs. 1-3) illustrates forms with distinctively larger antapical processes not unlike those of *Litosphaeridium siphoniphorum* (Cookson & Eisenack). Because of the larger size of this process she has incorrectly considered it to represent a second portion of the central body and has erected a new genus diagnosed as possessing bipartite cysts. The forms from the London Clay, the holotype of *D. colligerum* and the specimen illustrated by Cookson & Eisenack (1961, pl. 2, fig. 9) are probably more typical of the species and show without doubt that the "posterior portion of the shell" is in fact an enlarged antapical process. This species has been recorded from the Upper Cretaceous (probably Senonian) and Eocene of Australia, and in England only from the Eocene.

This species is easily distinguishable from all other types of dinoflagellate cysts.

OTHER SPECIES

The following species is here tentatively referred to the genus *Diphyes* on the basis of the numerous processes and single distinctive antapical process :

?*Diphyes monstuosum* (Tasch, McClure & Oftedahl 1964). Lower Cretaceous ; U.S.A.

Genus *DUOSPHAERIDIUM* nov.

DERIVATION OF NAME. Latin, *duo*, two ; *sphaera*, ball—with reference to the biospheroidal form of the test.

DIAGNOSIS. Proximate cyst composed of two more or less spheroidal parts, neither bearing processes. Anterior part with apical archaeopyle. Posterior part similar in shape with small circular antapical opening present.

TYPE SPECIES. *Diphyes nudum* Cookson 1965. Upper Eocene ; Australia.

REMARKS. The type species was formerly placed in the genus *Diphyes* by Cookson (1965) because of the apparent resemblance of its posterior part to the antapical process of *Diphyes colligerum*. However, the latter is a chorate cyst whereas the former is proximate, a difference considered by the authors to be of profound significance in the development history of dinoflagellate cysts and thus to preclude classification in the same genus.

Genus *TANYOSPHAERIDIUM* nov.

DERIVATION OF NAME. Greek, *tanyo*, long or stretched out ; *sphaera*, ball—with reference to the elongate nature of the central body exhibited by this genus.

DIAGNOSIS. Chorale cysts with elongate central body composed of endophragm and periphragm, the latter also forming the processes. Processes cylindrical, open distally and arranged in more or less regular circular manner around central body. Number of processes variable, usually one or two (occasionally three) per plate area. Archaeopyle apical.

TYPE SPECIES. *Tanyosphaeridium variecalamum* sp. nov. Upper Cretaceous (Cenomanian) ; England.

REMARKS. The marked feature of this genus is the elongate nature of the central body. Although the processes are arranged in a distinct circular manner on the surface of the central body, the tabulation is difficult to determine. The number of antapical processes, however, appears to be 3 or 6. Usually there is one or two processes per plate area, but occasionally three may be present. Neither a detached apical region nor a complete specimen has, so far, been observed.

Tanyosphaeridium variecalamum sp. nov.

Pl. 6, fig. 7 ; Text-fig. 20

DERIVATION OF NAME. Latin, *varius*, different ; *calamus*, reed—with reference to the rather variable extremities of the processes.

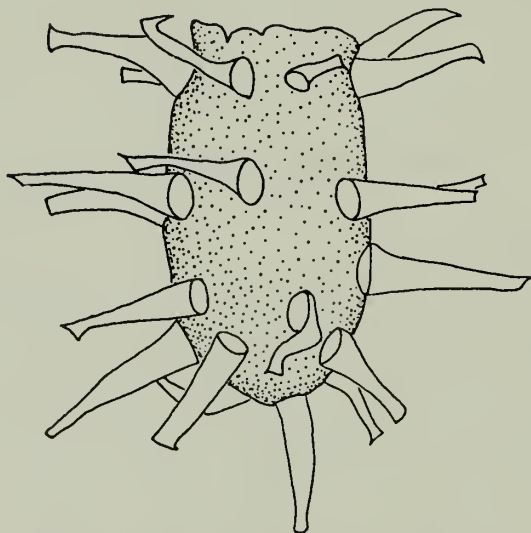


FIG. 20. *Tanyosphaeridium variecalamum* sp. nov. Holotype, lateral view, showing the circular arrangement of processes around the central body. $\times$ c. 1450.

DIAGNOSIS. Elongate central body with granular surface. Processes, moderate in number, cylindrical, expanding slightly distally and terminating with serrate, aculeate or truncated margin.

HOLOTYPE. Geol. Surv. Colln. slide PF.3035(2). Lower Chalk, H.M. Geological Survey Borehole, Fetcham Mill, Surrey, at 840 feet depth. Upper Cretaceous (Cenomanian).

DIMENSIONS. Holotype : length of central body 34μ , breadth 14μ , length of processes $12-16\mu$, number of processes 26. Range : length of central body $30-43\mu$, breadth $14-20\mu$, length of processes $12-24\mu$. Number of specimens measured, 13.

DESCRIPTION. The central body is composed of thin endophragm surrounded by granular periphragm. The processes are composed of smooth periphragm, and have an oval cross-section, there being characteristic oval areas on the surface of the central body beneath the processes, marking the initial divergence of the periphragm from the endophragm. The processes have fairly broad bases and taper distally before expanding slightly before terminating. Distally the processes may be truncated, terminate with one or two spines or splay out, the margin being serrate. The number of processes normally varies between 20 and 31, but one specimen has been observed with as many as 38.

An apical archaeopyle is always present, surrounded by 6 precingular processes. Medially there is a definite ring of 6 cingular processes and therefore 9-14 processes on the hypotract. The arrangement of the hypotractal processes is difficult to interpret ; however there appears to be either 3 or 6 antapical processes. The number of sulcal processes appears to be 5-7. This species is therefore variable in the number of processes it possesses and is able to have either one or two processes per plate in certain areas.

This species is present throughout the Cenomanian of England.

REMARKS. The only similar species is *T. isocalamus* (Deflandre & Cookson) from the Lower Cretaceous of Australia. The figures of the Australian form (Deflandre & Cookson 1955, pl. 2, figs. 7, 8) show that more processes are present than in *T. variecalamum* and that the extremities of the processes are more uniformly truncated.

***Tanyosphaeridium regulare* sp. nov.**

Pl. 3, fig. 3

DERIVATION OF NAME. Latin, *regularis*, according to rule—with reference to the regular arrangement of the processes.

DIAGNOSIS. Elongate central body with granular surface, bearing numerous tubular, usually curved processes. Processes terminating with somewhat serrate margin.

HOLOTYPE. B.M.(N.H.) slide V.51755(1). 270 feet above base of London Clay ; Whitecliff Bay, Isle of Wight.

DIMENSIONS. Holotype : length of central body 36.5μ , breadth of central body 23.5μ , length of processes $14-19\mu$, number of processes approximately 65. Range : length of central body $30-44\mu$, breadth of central body $21-24\mu$, length of processes $12-19\mu$. Number of specimens measured, 4.

DESCRIPTION. The periphragm of the central body is granular and bears a number of quite large tubercles. The periphragm of the processes is smooth. The processes have relatively broad bases, up to 4μ wide and taper distally being $1-1.5\mu$ wide for most of their length. At their distal extremities they widen slightly and have a somewhat serrate margin. The processes are arranged in circular series around the central body, indicating a reflected dinoflagellate tabulation. Two or, more rarely, three processes are present for each plate area.

T. regulare has been recorded from the London Clay of Whitecliff Bay and of Enborne, Berkshire.

REMARKS. The distinctive elongate nature of the central body of *T. regulare* is typical of this genus. *T. regulare* differs from *T. variecalamum* in having more processes, and from *T. isocalamus* comb. nov. in having slenderer processes with more complex terminations.

OTHER SPECIES

The following species are here attributed to the genus *Tanyosphaeridium* on the basis of the shape of the central body and the form of the processes :

Tanyosphaeridium ellipticum (Cookson 1965). Upper Eocene ; Australia.

Tanyosphaeridium isocalamus (Deflandre & Cookson 1955). Lower Cretaceous ; Australia.

Genus **HOMOTRYBLIUM** nov.

DERIVATION OF NAME. Greek, *homos*, same or similar ; *tryblion*, cup or bowl—with reference to the formation of two, almost equal, hemispheres after rupture of the cyst.

DIAGNOSIS. Sub-spherical chorate cyst with central body composed of thin endophragm and surrounding periphragm which gives rise to processes. Processes intratabular, cylindrical to tubiform, open distally, reflecting a tabulation of $3'$, $6''$, $6c$, $6'''$, $1p$, $1'''$ and 1 to 5s. Processes not in communication with cavity of the central body. Archaeopyle epittractal, suture running just above cingulum processes.

TYPE SPECIES. *Homotryblium tenuispinum* sp. nov. Eocene ; England.

DESCRIPTION. The genus *Homotryblium* is unusual in possessing an epittractal archaeopyle which has a compound operculum composed of the apical and precingular plate series. It is an easily recognizable genus because of the nature of this archaeopyle and the possession of only 3 apical processes. Dinoflagellate cysts possessing epittractal archaeopyles are rare. *Rhaetogonaulax* gen. nov. and *Dichadogonyaulax* gen. nov. are both described by Sarjeant, in a later section, as possessing epittractal archaeopyles ;

***Homotryblum tenuispinosum* sp. nov.**

Pl. 4, fig. 11 ; Pl. 12, figs. 1, 5, 7 ; Text-fig. 21

DERIVATION OF NAME. Latin, *tenuis*, thin; *spinosus*, thorny—with reference to the rather slender processes.

DIAGNOSIS. Spherical central body with wall composed of thin layers—smooth inner endophragm, outer strongly granular periphragm. Processes erect or curved, tubiform, simple, open distally with serrate or aculeate margin, rarely perforate. Width of processes variable.

HOLOTYPE. B.M.(N.H.) slide V.51756(1). Metropolitan Water Board Borehole No. 11 at 53 feet depth, London Clay ; Enborne, Berkshire.

DIMENSIONS. Holotype : diameter of central body 41 by 48 μ , length of processes 20–25 μ . Range : diameter of central body 41–57 μ , length of processes 13–32 μ . Number of specimens measured, 8.



FIG. 21. *Homotryblum tenuispinosum* sp. nov. A specimen from the London Clay, antapical view. $\times$ c. 950.

DESCRIPTION. The processes are restricted to one per plate area and indicate a reflected tabulation of 3', 6", 6c, 5"', 1p, 1'''' and 1-5s. The equatorial and sulcal processes are frequently more slender than the others. Distally the processes often have a margin bearing short bifid aculei. The length of the processes is about half the diameter of the central body. The margin of the archaeopyle is interrupted on the epitract by a short projection, the sulcal tongue (Evitt). This has a corresponding sulcal notch on the hypotract. The number of sulcal processes varies from 1 to 5. In some specimens the plates readily separate, save for the three apicals which have never been observed as individual plates.

H. tenuispinosum sp. nov. has only been recorded from the London Clay of England.

REMARKS. From the nature of the archaeopyle, the coarsely granular wall and the tabulation, *H. tenuispinosum* is distinct from all previously described species.

***Homotryblium pallidum* sp. nov.**

Pl. 12, figs. 4, 6 ; Text-fig. 22

DERIVATION OF NAME. Latin, *pallidus*, pale—with reference to the rather light colour of the central body after staining.



FIG. 22. *Homotryblium pallidum* sp. nov. A specimen from the London Clay. Internal view of the epitRACTAL operculum ; slender acuminate ancillary processes are present. $\times$ c. 950.

DIAGNOSIS. Sub-spherical to ovoidal central body composed of thin inner endophragm and granular periphragm. Processes of variable width, simple, tubiform, forming a circle where they arise from central body. Archaeopyle epittractal and processes reflecting generic tabulation.

HOLOTYPE. B.M.(N.H.) slide V.51756(1). Metropolitan Water Board Borehole No. 11, at 53 feet depth, London Clay ; Enborne, Berkshire.

DIMENSIONS. Holotype : diameter of central body 45 by 48 μ , length of processes up to 25 μ . Range : diameter of central body 40–49 μ , length of processes 16–34 μ . Number of processes 5. Number of specimens measured, 5.

DESCRIPTION. *H. pallidum* sp. nov. exhibits similar tabulation to *H. tenuispinosum* of 3', 6", 6c, 5''', 1p, 1'''' with almost invariably only three sulcal plates. The central body, which takes stain only slightly having a very thin wall, has granules up to 0.5 μ in height and 0.5 μ to 1.5 μ apart. The processes are cylindrical tubiform and in length closely approach the radius of the central body. Distally they are variable, in some specimens having an entire irregular margin, in others a serrate, aculeate or digitate margin. Besides the tubiform processes there are often present 1 to 5 slender small acuminate processes. The latter can occur on the hypo- or epittract.

This species has only been recorded from the London Clay of England.

REMARKS. *H. pallidum* differs from *H. tenuispinosum* in having a thinner wall, generally broader processes with more variable distal margins, and a well marked proximal circle where they arise from the central body. It also differs by having some very slender acuminate processes. The specimens with processes having entire circular or serrate margins appear to be closely related to *Hystrichosphaeridium choanophorum* Deflandre & Cookson (1954) from the Miocene of Australia, although Gerlack (1961) recognized what appears to be an apical archaeopyle in this species.

Genus *CALLAIOSPHAERIDIUM* nov.

DERIVATION OF NAME. Greek, *kallaion*, cockscomb ; *sphaera*, ball—with reference to the crests or ribs on the surface of the central body.

DIAGNOSIS. Chorate cysts with sub-spherical central body composed of two layers. Processes intratabular and of two types : (i) cingular processes large and tubular, open distally, and (ii) apical, precingular, postcingular and sulcal processes solid. Antapical processes absent. Reflected tabulation inferred from arrangement of processes is 1' (–2'), 6", 6c, 5''', 1p, 0'''' and 0–1s. Thickenings of periphragm join all except cingular processes. Archaeopyle epittractal, suture just above cingular processes.

TYPE SPECIES. *Hystrichosphaeridium asymmetricum* Deflandre & Courteville 1939. Upper Cretaceous ; France.

REMARKS. The form of the processes, the epittractal archaeopyle and the absence of antapical processes make this a very distinctive genus. The thickenings of the periphragm joining the processes are also a noteworthy feature, though not peculiar to this genus.

Callaiosphaeridium asymmetricum (Deflandre & Courteville)

Pl. 8, figs. 9, 10 ; Pl. 9, fig. 2

1939. *Hystrichosphaeridium asymmetricum* Deflandre & Courteville : 100, pl. 4, figs. 1, 2.

DESCRIPTION. This species, previously recorded only from the Senonian flints of France, has now been observed in the Speeton Clay of Yorkshire (Hauterivian and Lower and Middle Barremian) and in the Cenomanian of Surrey. All specimens agree fairly well with the original description given by Deflandre & Courteville (1939).

In the Barremian forms the large tubular processes tend to be considerably less spinous than the Upper Cretaceous forms and more globular, especially along the ribs. The term globular refers to small spherical spaces between the endophragm and the periphragm. In the Cenomanian examples, the distal spines may measure up to 20 μ . A noticeable feature in many of the British examples, not commented on in the original description, is the elevation of the ribs joining the hypotractal processes to form quite well developed septa.

An archaeopyle is usually present, formed by the loss of the portion of epitract just above the tubular cingular processes. The five postcingular processes are joined by ribs forming a pentagon from which radiate ribs to the cingular processes. Along one of these ribs are usually situated two processes—one posterior intercalary and one sulcal. The apical region possesses a hexagon of 6 precingular processes and an apical process which is sometimes deeply divided and arises from the centre of the hexagon. The reflected tabulation therefore is : 1' (—2'), ? 6'', 6c, 5''', 1p, 0'''' and 0—1s.

DIMENSIONS. Holotype : diameter of central body about 40 μ , length of tabular processes 22–34 μ . Range of Speeton Clay forms : diameter of central body 34–43 μ , length of cingular processes 11–20 μ . Number of specimens measured, 4. Range of Cenomanian forms : diameter of central body 37–58 μ , length of cingular processes 10–32 μ . Number of specimens measured, 5.

OTHER SPECIES HITHERTO PLACED IN *HYSTRICHOSPHAERIDIUM*

The following species formerly attributed to *Hystrichosphaeridium* Deflandre 1937 are here removed from this genus and referred to the following genera :

Achomosphaera alcornu (Eisenack 1954). Oligocene ; E. Prussia, USSR.

Achomosphaera grallaeforme (Brosius 1963). Oligocene ; Germany.

?*Achomosphaera hirundo* (Eisenack 1958). Lower Cretaceous ; Germany.

Hystrichosphaera leptoderma (Maier 1959). Oligocene ; Germany.

?*Hystrichokolpoma xiphea* (Maier 1959). Oligocene ; Germany.

Cymatiosphaera membranacea (Philippot 1949). Oligocene ; Germany.

CONCLUSIONS

The characteristics and known stratigraphical distribution of the 10 genera here considered are summarized in the accompanying Table. At present, the stratigraphic distribution of the genera cannot be correlated coherently with the variation in structure. As more species are attributed to these genera and the stratigraphic range of each genus becomes better known perhaps evolutionary relationships will become more obvious.

At present no species belonging to these genera have been found earlier than the Middle Jurassic. Three genera are present in the Upper Jurassic ; *Polysphaeridium*, perhaps a primitive form, bearing numerous processes, and *Hystichosphaeridium* and *Oligosphaeridium* both reflecting similar tabulations and possessing 4 apical processes. From the latter two genera perhaps are derived the remaining genera with the exception of *Diphyes*. After the Jurassic, although the tabulation remained basically the same, the number of apical plates appears to have become more variable and is probably an important systematic character. The genera *Diphyes*, *Cordosphaeridium* and *Homotryblium* have not been recorded, with certainty, from the Mesozoic.

Dinoflagellate cysts belonging to the genera discussed are relatively abundant from the Upper Jurassic to the end of the Eocene, but appear to become less common thereafter. After more detailed morphological studies have been performed their importance to world-wide stratigraphy should be considerable.

TABLE 3

Genera	Tabulation	Form Archeopyle	Form of processes	Shape of central body	Stratigraphic Range
<i>Polysphaeridium</i>	Numerous processes	Apical	Hollow, open or closed	Sub-spherical	Upper Cretaceous-Eocene (Cenomanian-Ypresian) Middle Jurassic-?Pleistocene
<i>Hystriochosphaeridium</i>	4' (-5'), 6'', 6c, 5-6''', 1p, 1'''' and xs.	Apical	Tubular	Sub-spherical	Upper Jurassic-Oligocene (Upper Jurassic-?Pliocene)
<i>Oligosphaeridium</i>	4', 6'', 5-6''', 1p, 1''''	Apical	Tubular	Sub-spherical	Upper Jurassic-Ypresian
<i>Callaiosphaeridium</i>	1' (-2'), 6'', 6c, 5''', 1p, 0'''' and 0-1 s	Epitractal	Cingular processes tabular, remainder are solid	Sub-spherical	Upper Jurassic-Upper Cretaceous Barremian-Senonian
<i>Litosphaeridium</i>	3', 6'', 5''', 1p, 1'''' and xs	Apical	Tubular	Sub-spherical	Lower Cretaceous-Upper Cretaceous Albian-Cenomanian (Albian-?Ypresian)
<i>Tanyosphaeridium</i>	Numerous processes 3'''' or 6''''	Apical	Tubular	Elongate	Lower Cretaceous-Eocene Ypresian
<i>Perissosphaeridium</i>	4', 6'', xc, 5''', 1p, 1'''' and xs	Apical	Tubular with closed cingular and sulcal processes	Sub-spherical	Lower Cretaceous-Eocene-Ypresian
<i>Diphyes</i>	Numerous processes 1''''	Apical	Hollow, open or closed. Large antapical processes	Sub-spherical	Eocene Ypresian (?Lower Cretaceous-Ypresian)
<i>Cordosphaeridium</i>	1', 6'', 6c, 6''', (1p), 1'''' and xs	Apical	Tubular and solid	Sub-spherical	Eocene Ypresian-Oligocene (?Lower Cretaceous-?Miocene)
<i>Homotryblum</i>	3', 6'', 6c, 6''', 1p, 1'''' Epitractal and 1-5 s	Epitractal	Tubular	Sub-spherical	Eocene? Ypresian

The character and known distribution of "hystriochospheres" with tubular processes. The stratigraphic range first shown is the confirmed one, and that shown in parenthesis is tentative.

VI. DINOFLAGELLATE CYSTS WITH *GONYAULAX*—TYPE TABULATION

By W. A. S. SARJEANT

INTRODUCTION

The dinoflagellate genus *Gonyaulax* was originally proposed by Diesing (1866) in the following terms :

"Animalcula solitaria libra symmetrica. Corpus immutabile, ovatum, ecaudatum, ciliatum, lorica, tabulata, sulco, hiante transversali in pagina dorsali obliquo in pagina ventrali bis geniculato et altero longitudinali, ab anfracto anteriori sulci transversalis ad extremitiatum anticam excurrenti, tripartita inclusum cili e sulcis prominentibus. Os terminale. Flagellum unum pone os. Anus Ocellus nullus. Partitio ignota. Mariolae."

The type species selected was *G. spinifera* (Claperide). An amended and much fuller diagnosis was subsequently proposed by Kofoed (1911) :

"Body variously shaped, spheroidal, polyhedral, broadly fusiform, elongated with stout apical and antapical prolongations, or dorsoventrally flattened. Apex rounded or truncate symmetrically or asymmetrically, never acutely symmetrically pointed. Antapex rounded, flattened, or pointed symmetrically or asymmetrically. Girdle usually equatorial, descending, displaced distally one to seven times its own width, and sometimes with slight overhang. Transverse furrow impressed or not ; longitudinal furrow usually slightly indenting the epitheca, often flaring distally, well developed, reaching to or approaching the antapex. Thecal wall consisting of one to six apical plates (1'-6'), none to three anterior intercalaries (1a-3a), six precingulars (1"-6"), six girdle plates (1g-6g), six postcingulars (1'''-6'''), one posterior intercalary (1p) and one antapical (1'''). The longitudinal furrow occupies the whole of the ventral area, which slightly indents the epitheca and consists of one anterior, about four intermediate, and one posterior plate. The midventral plate (1') of the apical series is usually a narrow plate extending posteriorly to a junction with the anterior plate of the ventral area, thus parting precingulars 1" and 6". When guarded by lateral ridges it simulates an anterior extension of the longitudinal furrow. It bears at its apex a delicate extension, the closing platelet which cover the apical region.

Surface smooth or rugose with major thickenings along suture lines and minor ones on plates forming a regular or irregular polygonal mesh of varying size, often with vermiculate longitudinal elements predominating, sometimes spinulate. Furrows with or without lists which in many species are ribbed or spinulate. One or more antapical spines sometimes present, rarely with sheathed spines of the *Ceratocorys* type. Plates porulate, with pores in centres, angles or nodes of the mesh. A peculiar large ventral pore occurs to the right of the midventral line, usually near the suture between apical 1' and the plate to its right. Theca divided obliquely in fission. Ecdysis frequently seen. Chromatophores yellow to dark brown, often dense. In fresh, brackish and marine waters from boreal to tropical regions."

Fossil forms, from the Upper Jurassic (Oxfordian) of France, were first attributed to this genus by Deflandre (1938). A tabulation pattern corresponding exactly to that of *Gonyaulax* was found to be exhibited by four species, which were named *G. jurassica*, *G. cladophora*, *G. eisenacki*, and *G. pachyderma*. A feature noted was the frequent absence of precingular plate 3", but the significance of this was not immediately recognized. A subsequent study by Deflandre of French Kimmeridgian sediments yielded further new species with the characteristic tabulation: and subsequent studies by various authors showed that fossils with a tabulation of this type were present from the Upper Triassic to the Oligocene, attaining greatest abundance in the Upper Jurassic and Lower Cretaceous.

A number of other genera with a corresponding or closely similar tabulation have since been proposed. The genus *Ctenidodinium* was proposed by Deflandre (1938) for Upper Jurassic forms having a strong, denticulate crest on the posterior margin of the cingulum, but with only a low ridge on its anterior margin. These forms split by schism along the line of the cingulum. Klement (1960) demonstrated that the tabulation of these forms corresponded to that of *Gonyaulax* and proposed abandonment of the name *Ctenidodinium*.

The genus *Lithodinia* was formulated even earlier (Eisenack 1935) for forms with a partially silicified shell from the Middle Jurassic (Dogger) of the Baltic. Subsequently Eisenack (1961) stated that he considered *Lithodinia* to be congeneric with *Gonyaulax*. The author was courteously allowed to examine the genotype of *Lithodinia* during a visit to Tübingen in 1962; the tabulation certainly corresponds closely to the *Gonyaulax* pattern.

The genus *Microdinium* was proposed by Cookson & Eisenack (1960) for forms having a tabulation pattern as follows; 1', 6", ?6c, 6''', 1p, 1''', the shell opening by loss of the apical plate. This tabulation accords with that specified by Kofoed (1911) and the genus is thus technically invalid; however, the majority of fossil species attributed to *Gonyaulax* have three to four apical plates.

The genus *Hystrichosphaera*, which has a *Gonyaulax*-type tabulation, is treated with in an earlier section. There are in addition six other described fossil genera showing a tabulation resembling, but not exactly corresponding to, that of *Gonyaulax*:

Cryptarchaeodinium Deflandre 1939, described from the French Upper Jurassic (Kimmeridgian), has the tabulation 4', 6", 7''', 1-?2p, ?1'''. This differs from that of *Gonyaulax* in the presence of an extra postcingular plate and in the presence of three plates (not yet clearly designated) in the antapical region.

Eisenackia Deflandre & Cookson 1955, described from the Lower Tertiary of Australia, has the tabulation ?3', 6", ?6c, 6''', 1-2p, 1'''. It differs from *Gonyaulax*, and corresponds to *Cryptarchaeodinium*, in having three plates in the antapical region, but differs from the latter genus in the possession of only two or three apical plates.

Leptodinium Klement 1960, described from the Upper Jurassic of Australia, has the tabulation 4', 6", ?6c, 5''', 1p, 1'''. It differs from *Gonyaulax* in the lack of any anterior intercalary plate and the presence of one fewer postcingular plate.

Pluriarvalium Sarjeant 1962, from the Upper Jurassic of England, has the tabulation 5', 1-3a, 6'', 6c, 6''', 1p, 1p.v., 1-?6p.c., 1'''''. It is characterized by possession of a posterior circle of small plates surrounding the antapex.

Glyphanodinium Drugg 1964, from the Paleocene of California, has the tabulation ?1', 5'', 6c, 6''', 1p, 1p.v., 1'''''. It is distinguished by the possession of only five precingular plates and the lack of an anterior intercalary plate.

There are in addition a number of genera whose tabulation is incompletely known but which appear comparable to the *Gonyaulax* type. *Eodinia* Eisenack 1936, from the Middle Jurassic of Germany, has a thick, porate wall and shows little sign of tabulation; there is no true cingulum, a helicoid suture being present instead. Comparison to the *Gonyaulax*-type cysts is afforded by the overall shape and the presence of an apical horn.

Rhynchodiniopsis Deflandre 1935, from the Upper Cretaceous of France, has raised, denticulate crests with spines arising at points of crest junction around the transverse furrow. The surface is reticulate: the tabulation undetermined. In shape and presence of an apical horn, it compares with the fossil cysts of *Gonyaulax* type: there are no apparent distinguishing characters.

Raphidodinium Deflandre 1936, from the Upper Cretaceous of France, has about a dozen spines arising at crest nodes, these spines being of sufficient length to render this a chorate cyst. Sutures are, however, present: the tabulation has not been determined.

Hystriodinium Deflandre 1935, again from the Upper Cretaceous of France, is another spinose form, the spines arising from sutures in considerably greater numbers. The tabulation appears comparable to that of *Gonyaulax* but has hitherto remained undetermined.

Belodinium Cookson & Eisenack 1960, from the Upper Jurassic of Australia, has a circular cingulum, plates differentiated by raised crests, an apical horn and a "flattened, membranous expansion" on the hypotract. This genus appears inadequately characterized. This comment applies equally to *Carpodinium* Cookson & Eisenack 1962b, from the Lower Cretaceous of Australia whose tabulation is incompletely known and whose other characters in no wise differ from those specified for *Gonyaulax*.

Heliodinium Alberti 1961, from the Lower Cretaceous of Germany, resembles *Hystriodinium* but has flattened, dagger-like processes arising from the crests. The tabulation is again undetermined but appears closely similar to that of *Gonyaulax*.

There are thus a considerable number of genera of fossil dinoflagellates which possess or approach the *Gonyaulax* tabulation pattern. Those forms directly allocated to the genus *Gonyaulax* were originally considered to be the fossil remains of the motile stage of that genera. It was nonetheless recognized that the shell wall characteristically contained an opening of some kind, formed by median fission or by loss of a plate or a group of plates. Following the demonstration by Evitt (1961) that the occurrence of such openings (archaeopyles) indicated cysts, it became clear

that the fossil *Gonyaulax* species were in fact cysts. Subsequently Evitt & Davidson (1964) demonstrated from studies of modern dinoflagellates that the genus *Gonyaulax* formed cysts of more than one type, but certainly including chorate cysts attributable to the genus *Hystrichosphaera*; and Sarjeant (1965, text-fig. 3) showed that the arrangement of processes in the chorate Lower Cretaceous species *Oligosphaeridium* (formerly *Hystrichosphaeridium*) *vasiformum* indicated a *Gonyaulax*-type motile stage.

A somewhat confusing nomenclatural situation thus presents itself. On the one hand, it is now clear that a single modern dinoflagellate genus, with a constant tabulation, may form cysts which are of such distinctly different morphology as to merit classification into different form-genera; it is arguable, on this basis, that the cyst characters indicate different evolutionary lineages and fully justify splitting of the modern genus. On the other hand, should the modern genus be retained unamended, it might well be considered that retention of separate generic names for the fossil cysts, which are simply stages in the life cycle, is unjustifiable.

The terms of the "International Code of Botanical Nomenclature" recognize the existence of genera of three types—natural "Linnaean" genera; organ genera, representing either parts of plants or stages in their life cycles; and form genera, defined on morphology alone. Certain genera of dinoflagellate cysts may prove, as in the case of *Hystrichosphaera*, to have a determinable relationship to a living genus defined on its motile stage. However, it remains to be proved that a particular cyst type can be produced *only* by one particular motile type; it is entirely possible that the same cyst type might be produced by related, but different, motile types. The dinoflagellate cysts, whether recent or fossil, are best treated as form genera and species, unless or until special provisions are framed for their treatment.

These problems have been discussed at length by Deflandre (1964), Evitt & Davidson (1964) and Norris (1965). A first step towards their solution was taken by Deflandre (1964 : 5) :

" . . . je place dans le genre *Gonyaulacysta* nov. gen. (générotype : *Gonyaulax jurassica* Defl. 1938) toutes les espèces fossiles à tabulation de *Gonyaulax* représentées par des thèques à côtes saillantes plus ou moins ornementées (pectinées, épineuses, denticulées etc . . .) munie d'un archéopyle (3ième plaque pré-équatorial)."

This proposal provides a partial answer to the problem; however, the fossil species previously classed into *Gonyaulax* include not only forms with a precingular archaeopyle formed by loss of plate 3", but also forms with apical, epittractal and cingular archeopyles. Moreover, the diagnosis remains too wide in terms of tabulation and overall morphology; forms like *Hystrichodinium* and *Heliodinium* would become homonyms, should their tabulation be shown to correspond to that of *Gonyaulax*. A more restricted diagnosis of *Gonyaulacysta* is therefore proposed in the section that follows; the status of the genera mentioned earlier is reviewed; and new genera are set up to accommodate species which do not accord with the revised concept of *Gonyaulacysta*, either in tabulation, ornamentation or mode of archaeopyle formation.

A. Genera with precingular archaeopyle

Genus *GONYAULACYSTA* Deflandre 1964 : 5

EMENDED DIAGNOSIS. Proximate dinoflagellate cysts, spherical, ovoidal, ellipsoidal or polyhedral, with the tabulation 3-4', 0-1a, 6'', 6c, 6''', 1p, 0-1 p.v., 1'''''. Cingulum strongly or weakly helicoid. Cingular plates (6c) well or poorly marked ; ventral surface may show division into additional small plates. Sulcus generally but not constantly extending onto epitract. Apical horn frequently, but not constantly present ; median and antapical horns lacking. Sutures in form of low ridges ; bearing crests of varied form (smooth denticulate or spinous ; perforate or imperforate) ; or marked by lines of spines of varied form. Height of spines or crests always less than $\frac{1}{4}$ of shell width. A precingular archaeopyle formed by loss of plate 3''. (Archaeopyle not always present.) Surface smooth, granular, nodose, punctate or reticulate.

TYPE SPECIES. *Gonyaulax jurassica* Deflandre 1938. Upper Jurassic (Oxfordian) ; France.

REMARKS. The generic diagnosis is emended to include reference to tabulation and to exclude forms characterized by very high crests, very long sutural spines, or a general spine cover. Forms with high crests are referred to *Heslertonia* gen. nov. ; forms with long sutural spines to *Heliodinium*, *Hystrichodinium* or *Raphidodinium* ; and forms with a general spine cover to *Acanthogonyaulax*. Forms according to this diagnosis but with an apical archaeopyle are referred to *Meiourogonyaulax* ; forms with an epittractal archaeopyle to *Rhaetogonyaulax* and *Dichadogonyaulax* ; and forms with a cingular archaeopyle to *Ctenidodinium*.

Gonyaulacysta gongylos sp. nov.

Pl. 13 figs. 1, 2 ; Text-fig. 23.

1961. *Gonyaulax* sp., Sarjeant : 97, pl. 13, fig. 15 ; text-fig. 6.

DERIVATION OF NAME. Greek, *gongylos*, ball, in reference to the spherical shape.

DIAGNOSIS. A *Gonyaulacysta* having an almost spherical theca, with short blunt apical horn. Tabulation 4', 1a, 6'', 7c, 6''', 1p, 1'''' ; plate boundaries usually bearing low, denticulate crests. Plate 1' elongate and corresponding to anterior prolongation of sulcus ; plate 4' very small, occupying horn tip. Plate 1''' reduced and elongate ; its boundary with sulcus not marked by a crest. Sulcus and cingulum both relatively broad ; cingular plate 7c small and pentagonal in shape.

HOLOTYPE. B.M.(N.H.) slide V.51708(2). Lowest Oxford Clay ; Castle Cliff, Scarborough, Yorks. Upper Jurassic (Lower Oxfordian).

DIMENSIONS. Holotype : overall length 47 μ , length of horn 5 μ ; overall breadth 45 μ ; breadth of cingulum c. 5 μ . The few other specimens seen proved too severely damaged for measurement, but appear of comparable dimensions.

DESCRIPTIONS. Theca almost spherical, but having a somewhat polygonal appearance because of the angularly set crests. The horn is tipped by plate 4' ; extensions of plates 1-3' form its base. The anterior intercalary plate, 1a, is quadrate and separated from the horn by plate 3'. Of the six precingular plates, plate 6'' is reduced, plate 3'' notably large and forming the anterior dorsal surface. It is arguable whether there are five or six postcingular plates, since plate 1''' is defined only by the angles formed by plates 2''' and 1p with the furrow and sulcus. Plate 3''' is large and forms the posterior dorsal surface : plate 2'' is reduced to accommodate the quadrate posterior intercalary plate. The antapex is occupied by a single polygonal plate.

The cingulum is broad and laevorotatory, its two ends differing in antero-posterior position by the cingulum's width. A pentagonal plate is present between the sulcus and the more posterior end of the cingulum ; this is here designated plate 7c, but since its form does not correspond with that of the other cingular plates, a special name might be merited. The sulcus is narrow in its anterior portion, broadening to contact with the cingulum and thenceforward remaining of constant breadth in its posterior portion.

The surface of the periphragm is generally smooth, but bears a sparse scatter of coarse granules. The crests are strong but low, with well marked denticulations, resembling in form crest type f. of *Gonyaulacysta jurassica* (cf. Sarjeant, 1961, text-fig. 1).

REMARKS. *Gonyaulacysta gongylos* sp. nov. is an unusually small species characterized by its overall shape, its apical tabulation, and the presence of plate 7g. Re-examination of the holotype under a more powerful microscope has led to a fuller elucidation of the structure, in particular with regard to the crest form and the pattern of postcingular plates (a presumed plate boundary being shown to be merely a fold).

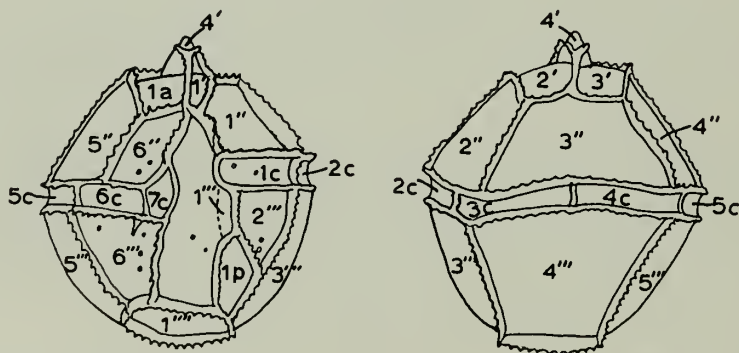


FIG. 23. *Gonyaulacysta gongylos* sp. nov. Tabulation. Left, ventral view ; right, dorsal view. $\times$ c. 800.

This species remains infrequent, only a very few severely damaged specimens having been encountered subsequently. For this reason also, the character of the archaeopyle remains to be confirmed; allocation to *Gonyaulacysta* is made on the basis of tabulation and general morphology. It shows a similarity to a group of Upper Jurassic–Lower Cretaceous species *Gonyaulacysta jurassica*, *G. eisenacki*, *G. cretacea* and *G. helicoidea* in crest form and in the reduction of plate 1", but differs from them in shape and presence of plate 7c.

***Gonyaulacysta palla* sp. nov.**

Pl. 13, figs. 3, 4; Text-fig. 24

DERIVATION OF NAME. Greek, *palla*, ball, in reference to the overall shape.

DIAGNOSIS. A *Gonyaulacysta* with almost spherical theca and prominent apical horn. Tabulation 4', 1a, 6", ?6c, ?7"', 1p, 1''''; plate boundaries demarcated by crests formed of very short spines arising from low ridges. Plate 1' elongate, occupying anterior prolongation of sulcus and relatively large; plate 4' small, occupying horn tip. Sulcus and cingulum of moderate breadth. Plate 1''' small and quadrate: posterior intercalary plate correspondingly small. Plate 2''' somewhat larger than plate 1''', but remaining markedly smaller than other postcingular plates. Number of postcingular plates probably seven, but presence of crest between plates 4''' and 5''' not confirmed.

HOLOTYPE. B.M.(N.H.) slide V.51718(2). Speeton Clay, Shell West Heslerton Borehole No. 1, West Heslerton, Yorks., at 42.50 metres depth. Lower Cretaceous (Lower Barremian).

DIMENSIONS. Holotype: overall length 62μ , length of horn, 10μ ; overall breadth 50μ ; breadth of cingulum $c.4\mu$. Range of dimensions observed; overall lengths $60\text{--}64\mu$, overall breadths $46\text{--}52\mu$.

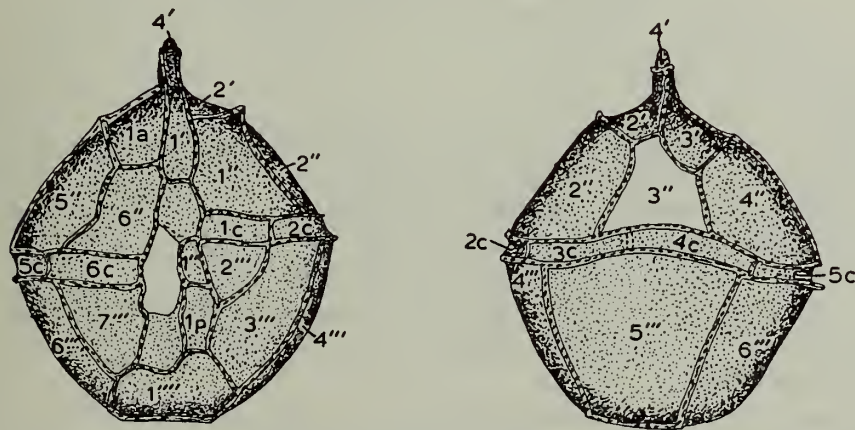


FIG. 24. *Gonyaulacysta palla* sp. nov. Tabulation. Left, ventral view; right, dorsal view. $\times c. 800$.

DESCRIPTION. Theca spherical, relatively thin-walled and apparently fragile ; of some 20 specimens seen, all had suffered damage additional to archaeopyle formation. The holotype is the best-preserved, but nonetheless shows a tear in median ventral position. Surface densely granular, the granulation rendering the low crests difficult to distinguish in lateral positions.

Apical horn slender and relatively long, accounting for about $\frac{1}{4}$ th of the thecal length. Its tip is formed by plate 4', its base by plates 1 to 3'. Six precingular plates, with plate 6' reduced to accommodate the anterior intercalary plate. Either six or seven postcingular plates ; presence of the presumed boundary between plates 4" and 5" could not be completely verified in any specimen seen, through a combination of damage and unfortunate orientation. Plates 1''' and 1p are both small : plate 2''' is also reduced and does not have a boundary with the antapical plate. The antapical plate has the appearance of being inclined towards the ventral face, but this may simply result from compression.

The cingulum is of moderate breadth and strongly laevorotatory, its two ends differing in antero-posterior position by about one and a half times its breadth. The number of cingular plates is doubtful. The sulcus is short and of moderate breadth.

All specimens seen have a precingular archaeopyle, formed by loss of plate 3".

REMARKS. In its combination of overall morphology and tabulation, *Gonyaulacysta palla* differs from all other described species. The most closely similar species is *G. ambigua* (Deflandre), which has a similarly spherical shape and crests of comparable character, but differs in having no comparable apical horn and a different ventral tabulation.

Gonyaulacysta axicerastes sp. nov.

Pl. 13, figs. 11, 12 ; Text-fig. 25

DERIVATION OF NAME. Greek, *axon*, axis ; *kerastes*, horned—hence, axially horned.

DIAGNOSIS. A *Gonyaulacysta* having a spheroidal shell with apical pericoel crowned by slender horn arising from periphragm. Second short horn, formed from both membranes, present at antapex. Tabulation ?4', 1a, 6", 6c, 6''', 1p, 1'''' ; plate boundaries bearing high delicate crests. Cingulum and sulcus relatively narrow, sulcus somewhat sinuous and broadening posteriorly.

HOLOTYPE. B.M.(N.H.) slide V.51727(1). Speeton Clay, Shell West Heslerton Borehole No. 1, West Heslerton, Yorks., at 39 metres depth. Lower Cretaceous (Middle Barremian).

DIMENSIONS. Holotype : overall length 71μ , breadth 60μ ; shell length 50μ , breadth 52μ ; width of cingulum $c.5\mu$; length of apical horn, 8μ ; length of antapical horn, 7.5μ . Other specimens seen too damaged for measurement.

DESCRIPTION. Shell spheroidal, slightly broader than long, with epittract surmounted by a dome-like outgrowth of the periphragm enclosing an apical pericoel. A slender, furcate horn arises from the apex. The dome-like structure arises from the confluent crests of the plates on the apical portion of the epittract; position of three-? four apical plates and an anterior intercalary plate are indicated by dimples in this structure. Six precingular plates are present, plate 6'' being of reduced size. Six postcingular plates are likewise present, with plate 1''' slightly reduced to accommodate the posterior intercalary plate. A polygonal plate occupies the antapex; from its centre arises a short, blunt antapical process. Slender spines at the angles sustain the crests surrounding the antapex; these crests are not connected to the antapical process.

The cingulum forms a strong laevorotatory spiral such that its two ends differ in antero-posterior position by more than twice its width. It is divided into six cingular plates. The sulcus is sinuous rather than sigmoidal: a median section along its line would touch the two ends of the cingulum but would not cut them. It is of moderate breadth in its epittractal portion, but widens as it approaches the antapex.

The crests are high and delicate, with denticulate edges; they are irregularly perforate, the perforations being so fine as to be almost imperceptible at high magnifications ($\times 1,000$). The surface bears an irregular, sparse scatter of coarse tubercles, but is otherwise smooth.

No archaeopyle has been observed.

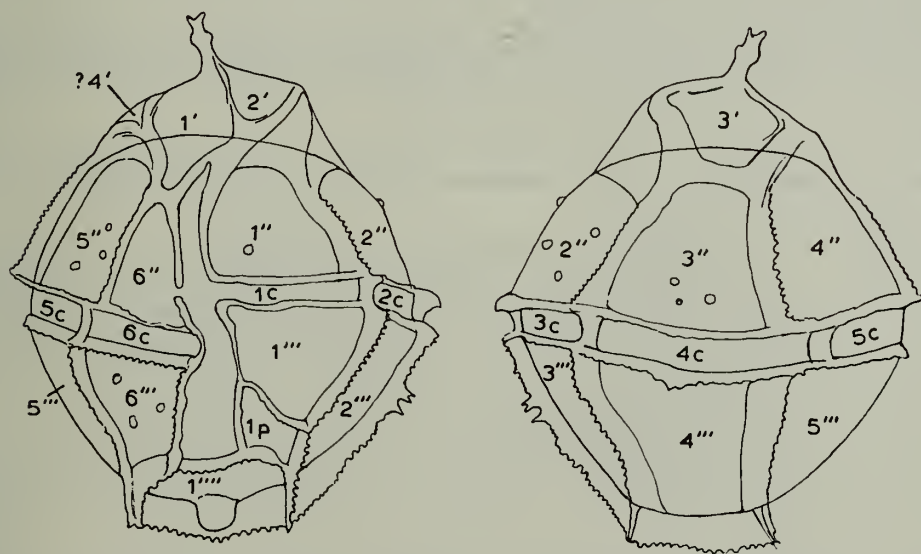


FIG. 25. *Gonyaulacysta axicerastes* sp. nov. Tabulation. Left, ventral view; right, dorsal view. $\times c. 1000$.

REMARKS. In its possession of an apical pericoel, surmounted by a horn, *Gonyaulacysta axicerastes* differs from all other species of the genus except *G. cassidata*. It differs from *G. cassidata* in the form of the central shell, which is more ovoid in the latter species ; the less markedly sigmoidal form of the cingulum ; the more slender shape of the apical horn ; the detail of ventral tabulation ; and the possession of an antapical horn. *Scriniodinium apaletum* Cookson & Eisenack 1960, from the Upper Jurassic of Australia, has an apical horn and pericoel of similar form but differs in having an antapical pericoel also. The tabulation of *Scriniodinium apaletum* has not yet been fully described.

***Gonyaulacysta helicoidea* (Eisenack & Cookson)**

Pl. 13, figs. 7, 8 ; Pl. 15, figs. 8, 9 ; Text-fig. 26

1960. *Gonyaulax helicoidea* Eisenack & Cookson : 2, pl. 1, figs. 4-9.

EMENDED DIAGNOSIS. A *Gonyaulacysta* with spheroidal to ovoidal theca surmounted by blunt apical horn. Epittract longer than hypottract ; antapex flattened. Tabulation : 4', 1a, 6", 6c, 6"', 1p, ?1 p.v., 1''' ; plates bordered by denticulate crests, varying considerably both in height and character of denticulation. Cingulum strongly spiral : sulcus sigmoidal, plates 6" and 1''' roughly L-shaped. Surface bearing irregular scatter of tubercles.

HOLOTYPE. The specimen figured by Eisenack & Cookson (1960, pl. 1, fig. 4). I. C. Cookson Colln., Melbourne. Lower Cretaceous (Aptian or older) ; Lake Phillipson bore, South Australia, at 87 ft. 10 in.

MATERIAL (figured). B.M.(N.H.) slide V.51718(1), Speeton Clay, Shell West Heselton Borehole No. 1, West Heselton, Yorks., at 42.5 metres depth, Lower Cretaceous (Lower Barremian).

DIMENSIONS. Holotype : overall length 78 μ , breadth 56 μ . Range of Australian specimens : overall length 62-86 μ , breadth 48-67 μ . Figured specimen (Speeton Clay) : overall length 45 μ , breadth 45 μ ; shell length 38 μ , breadth 43 μ ; length of horn 7 μ . Range of English specimens : overall length 44-53 μ , breadth 42-46 μ .

DESCRIPTION. The shell shape varies from an ovoid to an oblate spheroid ; the length of the horn and the height and form of the crests are also very variable.

Of the four apical plates, plate 1' occupies the anterior prolongation of the sulcus : it is long and narrow. An elongate anterior intercalary plate is present alongside it. The four apical plates together form the apical horn, their crests being confluent at its tip. Six precingular plates are present, with plate 6" small, elongate, and roughly L-shaped. Six post-equatorial plates are present, plate 1''' being roughly axe-shaped, with broad anterior and narrow posterior portions. A quadrate posterior

intercalary plate is present. The single antapical plate is large and polygonal; the crests surrounding it are supported at their junctions by spines. A posterior ventral plate may be present, but if so, its anterior boundary is ill-defined.

The cingulum is relatively narrow and pronouncedly laevo-rotatory, its two ends differing in antero-posterior position by three times its width. The sulcus is markedly sigmoidal; a median dorso-ventral section would thus cut both ends of the cingulum. Six cingular plates appear to be present; the posterior end of the cingulum is separated from the sulcus by a small crescentic plate, poorly marked or indistinguishable in many specimens and thus excluded from the diagnosis. The crests crossing furrows lack denticles.

An irregular scatter of tubercles is present on the surfaces of the plates; the number, density and situation of these tubercles varies greatly between individuals.

A precingular archaeopyle is usually present, formed by loss of plate 3".

REMARKS. The diagnosis of *Gonyaulacysta helicoidea* is emended to include reference to the tabulation. This species is numerous in the assemblages from 39 and 42.5 metres depth in the Speeton Clay; although the English specimens are markedly smaller, there can be no doubt that they are conspecific with the Australian species.

A closely comparable species, *Gonyaulacysta cretacea* (Neale & Sarjeant 1962) is present in somewhat earlier horizons (99.25 metres—Hauterivian) in the West Heselton boring. This differs from *G. helicoidea* only in having a more markedly polygonal outline and in lacking tubercles. It seems probable that *G. cretacea* is ancestral to *G. helicoidea*.

The form from the Lower Cretaceous of New South Wales, figured by Deflandre & Cookson (1956, pl. I, fig. 6) as ?*Gonyaulax* sp. indet., may well be attributable to this species.

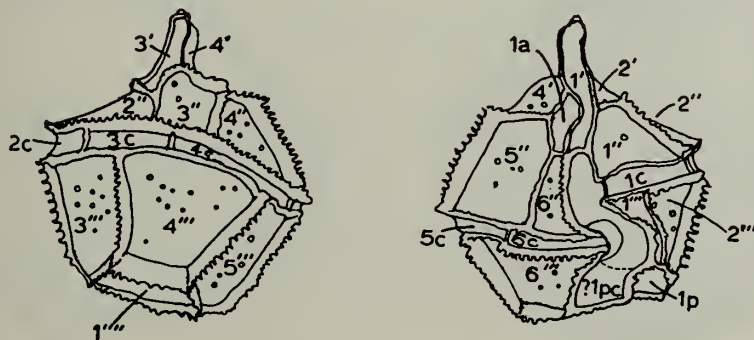


FIG. 26. *Gonyaulacysta helicoidea* (Eisenack & Cookson). Tabulation. Left, ventral view; right, dorsal view. $\times$ c. 800.

characteristic trifurcate appearance. There are four apical plates, plate 1' occupying the anterior prolongation of the sulcus and being unusually broad. Six precingular plates are present, the sixth being reduced to accommodate the anterior intercalary plate.

Six postcingular plates are present, plate 1''' being reduced to accommodate the posterior intercalary plate. A roughly quadrate posterior ventral plate separates the sulcus from the single large antapical plate.

The cingulum is of moderate breadth and forms a strong laevorotatory spiral such that its two ends differ in antero-posterior position by three times its breadth. It comprises certainly five, possibly six cingular plates. The sulcus is short and broad.

The surface is densely granular. In at least one specimen (figured), a very few short spines are present on the surface of the hypotract: spines are not present, however, on the holotype. The degree of granulation of the sulcus is markedly less than that of the rest of the surface.

A precingular archaeopyle, formed by loss of plate 3", is present in all specimens seen.

REMARKS. *Gonyaulacysta episoma* sp. nov. is characterized by its combination of shape, tabulation and crest character. *Gonyaulacysta nuciformis* (Deflandre 1938), from the Upper Jurassic, has a somewhat similar overall shape and degree of granulation, but the shell wall is thicker, the tabulation is less clear and the form of the crests is quite different. *Gonyaulacysta scotti* (Cookson & Eisenack 1958) an inadequately described species from the Upper Jurassic of Western Australia, has rather similar crests, but has a more markedly ovoidal shape and an apical horn of dissimilar type. *Gonyaulacysta tenuiceras* (Eisenack 1958) from the Aptian of Germany, has a horn and crests of somewhat similar character, but the crests are much higher and the tabulation is markedly different. A specimen figured as *G. tenuiceras* by Alberti (1961, pl. 11, fig. 7), from the Upper Barremian of Germany, may well be in fact *G. episoma*.

***Gonyaulacysta hadra* sp. nov.**

Pl. 14, fig. 1; Text-fig. 28

DERIVATION OF NAME. Greek, *hadros*, well-developed, bulky, stout—referring to the unusually large size.

DIAGNOSIS. A *Gonyaulacysta* with thick-walled, spherical to spheroidal shell and long, tapering apical horn. Tabulation 4', ?oa, 6", 6c, 6''', 1p, 1 p.v., 1''''; poorly marked by crests in form of very low ridges bearing well spaced, extremely abbreviate spinelets. Cingulum weakly spiral: sulcus short, confined to ventral region. Surface generally densely granular.

HOLOTYPE. B.M.(N.H.) slide V.51731(1). Speeton Clay, Shell West Heselton No. 1 Borehole at 19.25 metres depth, West Heselton, Yorks., Lower Cretaceous (Upper Barremian).

PARATYPE. B.M.(N.H.) slide V.51730(5). Same locality and horizon.

DIMENSIONS. Holotype : overall length 151μ , breadth 117μ . Shell length 117μ ; length of horn 34μ ; breadth of cingulum $c.7\mu$. Paratype : overall length 145μ , breadth $c.112\mu$; shell length 105μ ; length of horn 40μ ; breadth of cingulum $c.5\mu$. Range : overall length $c.140-155\mu$.

DESCRIPTION. This is an unusually large and very characteristic species, quite frequent at this horizon, some 20 specimens having been studied. The dense granulation and relatively inconspicuous character of the crests render the tabulation difficult to determine : Text-fig. 28 was prepared from study of several specimens and is unlikely to be accurate in detail. On most specimens, including the holotype, granules are absent from various small patches of the surface : this appears to result from damage. Granulation is consistently faint or lacking on the sulcus, which is somewhat sunken.

The test is spherical to spheroidal and composed of two distinct layers ; a fairly thin periphragm and a thicker endophragm. The endophragm bulges only into the base of the apical horn, so that the horn contains a cavity between the wall layers.

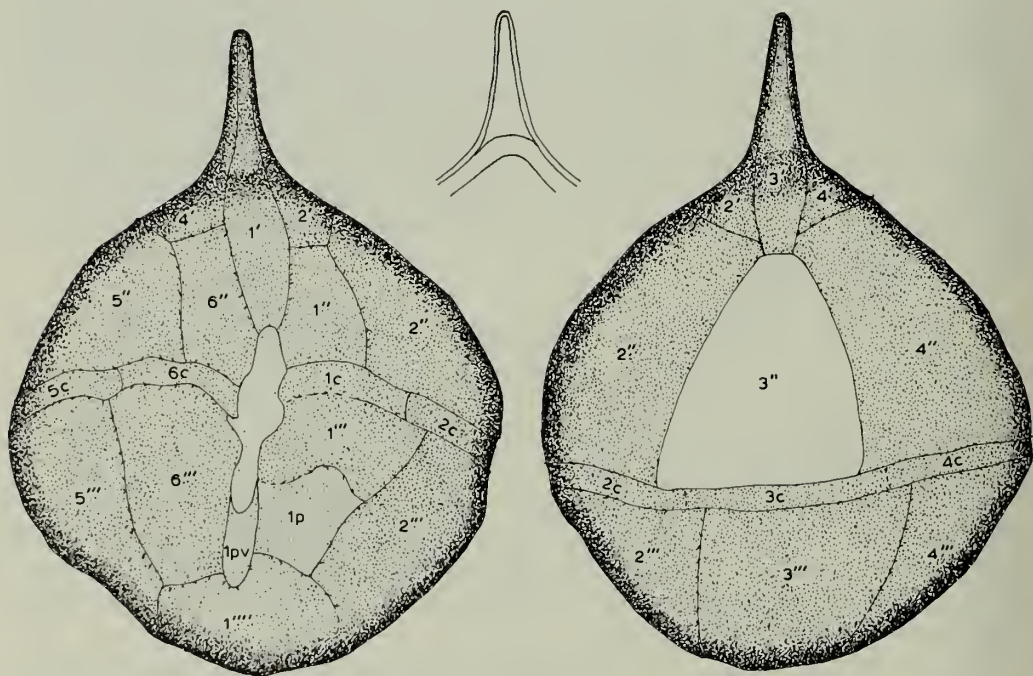


FIG. 28. *Gonyaulacysta hadra* sp. nov. Tabulation. Left, ventral view ; right, dorsal view. Insert : the wall structure at the apex, in diagrammatic section. $\times c. 550$.

Four apical plates are present, jointly forming the apical horn. Plate 1' is long and broad, occupying the anterior prolongation of the sulcus. An anterior intercalary plate could not be determined. Six precingular plates are present, plates 1" and 6" being reduced. There are also six postcingular plates, with plate 1''' reduced to accommodate the large posterior intercalary plate. A narrow posterior ventral plate separates the polygonal antapical plate from the sulcus.

The cingulum forms a feebly laevorotatory spiral, its two ends scarcely differing in antero-posterior position. The sulcus is short, extending only over the middle third of the ventral surface: it is widest at mid-point and tapers to anterior and posterior.

A precingular archaeopyle, formed by loss of plate 3", is present in all specimens seen.

REMARKS. In general form, tabulation and crest character, *Gonyaulacysta hadra* sp. nov. differs from all described species.

Gonyaulacysta orthoceras (Eisenack)

Pl. 14, figs. 5, 6; Text-fig. 29

1958. *Gonyaulax orthoceras* Eisenack: 388, pl. 21, figs. 3-14, pl. 24, fig. 1; text-figs. 2, 3.

1959. *Gonyaulax orthoceras* Eisenack; Gocht: 54, pl. 5, figs. 12, 13.

1961. *Gonyaulax orthoceras* Eisenack; Alberti: 6, pl. 11, figs. 1-3.

1963. *Gonyaulax orthoceras* Eisenack; Górka: 30, pl. 3, figs. 1-4.

EMENDED DIAGNOSIS. A *Gonyaulacysta* having an ovoidal theca of moderate wall thickness, with strong, tapering apical horn accounting for about one-fifth to one quarter of overall length. Tabulation 4', 1a, 6", ?6c, 7''', 1p, 1''''; plate boundaries outlined by low crests bearing very abbreviate spinelets. Cingulum strongly spiral, of moderate breadth: sulcus broad and extending to antapex. Surface of shell granular to tuberculate.

HOLOTYPE. The specimen illustrated by Eisenack (1958, pl. 21, fig. 5) from Preparation Ob. Apt. no. 32. Aptian glauconitic limestone, Deutschen Erdöl A.G., Erdölwerke Holstein, boring Marne, Feld Heide, North Germany, at 761-7 metres depth.

MATERIAL (figured). B.M.(N.H.) slide V.51730(3). Speeton Clay, Shell West Heselton Borehole No. 1, West Heselton, Yorks., at 19.25 metres depth. Lower Cretaceous (Upper Barremian).

DIMENSIONS. Holotype: overall length 95 μ , breadth 71 μ ; length of horn 22 μ . Range of German specimens: overall length 70-105 μ . Figured specimen: overall length 100 μ , breadth 80 μ ; length of horn c.20 μ ; width of cingulum c.5 μ . Range of English specimens; overall length 80-115 μ .

DESCRIPTION. Shell broadly ovoidal, with the hypotract rounded. The crests separating the four apical plates converge at the apex. Plate 1' occupies the anterior prolongation of the sulcus and is markedly elongate. Six precingular plates are present, with plate 6'' very reduced to accommodate an anterior intercalary plate. Seven postcingular plates are present, plates 1''' and 2''' being reduced to accommodate a rather indistinctly demarcated posterior intercalary plate. A single polygonal plate occupies the antapex.

The cingulum forms a laevorotatory spiral such that its two ends differ in antero-posterior position by over three times its width. The number of cingular plates appears to be six, but the crests separating them are poorly marked. The sulcus is of moderate breadth and extends from mid-point on the epitract to the antapex.

The shell wall is of moderate thickness and consists of two distinct layers. The apical horn is formed by the periphragm, the endophragm showing no outbulge; the horn is thus hollow and contains what is effectively an apical pericoel. The English specimens have a densely granular surface, but lack tubercles such as are present on the German specimens.

A precingular archaeopyle, formed by loss of plate 3'', is generally present.

REMARKS. The diagnosis is emended to include reference to the tabulation. In his original diagnosis, Eisenack figures two alternative tabulation patterns and

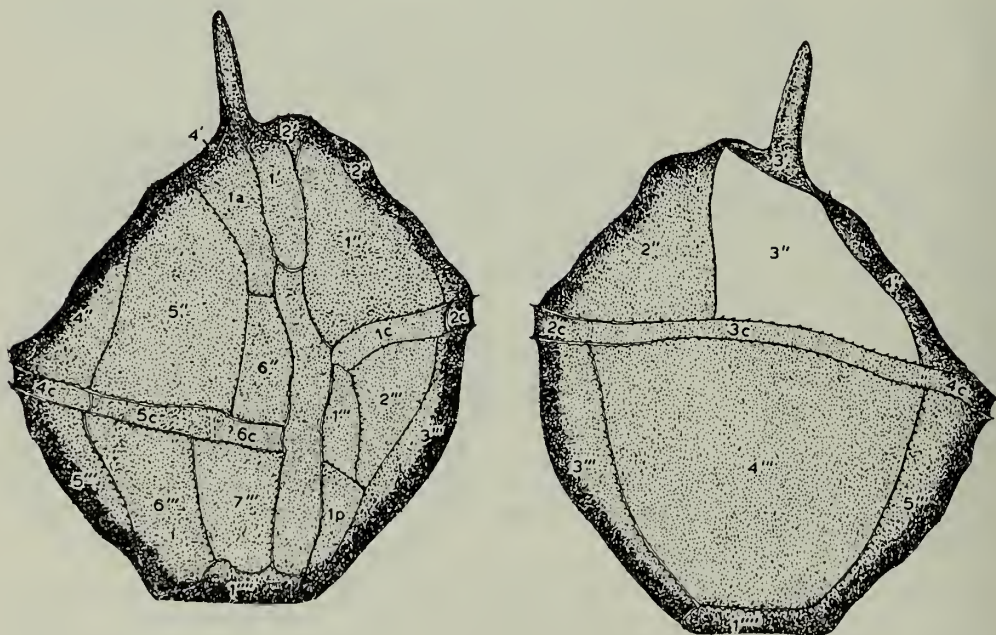


FIG. 29. *Gonyaulacysta orthoceras* (Eisenack). Tabulation. Left, ventral view; right, dorsal view. $\times$ c. 750.

expresses doubt as to which is correct ; he comments on the difficulty of distinguishing crests from folds. The tabulation presented in Eisenack's Text-fig. 3 agrees closely with that determined from the English specimens. The plate here designated as postcingular plate 1''' is figured, but not numbered ; Eisenack's plates 1''' to 6''' thus correspond to plates 2''' to 7''' of the scheme here adopted. The presence of anterior and posterior intercalary plates is confirmed.

Gonyaulacysta orthoceras (Eisenack 1958) is an abundant and characteristic Cretaceous species, having a known range from Upper Valanginian to Turonian. It is clearly distinguishable through its combination of shape, tabulation, and nature of crests : comparisons with other described species are discussed by Eisenack (1958 : 389) and Górka (1963 : 31).

***Gonyaulacysta aichmetes* sp. nov.**

Pl. 13, figs. 5, 6 ; Text-fig. 30

DERIVATION OF NAME. Greek, *aichmetes*, spearman, warrior ; referring to the pronounced apical horn.

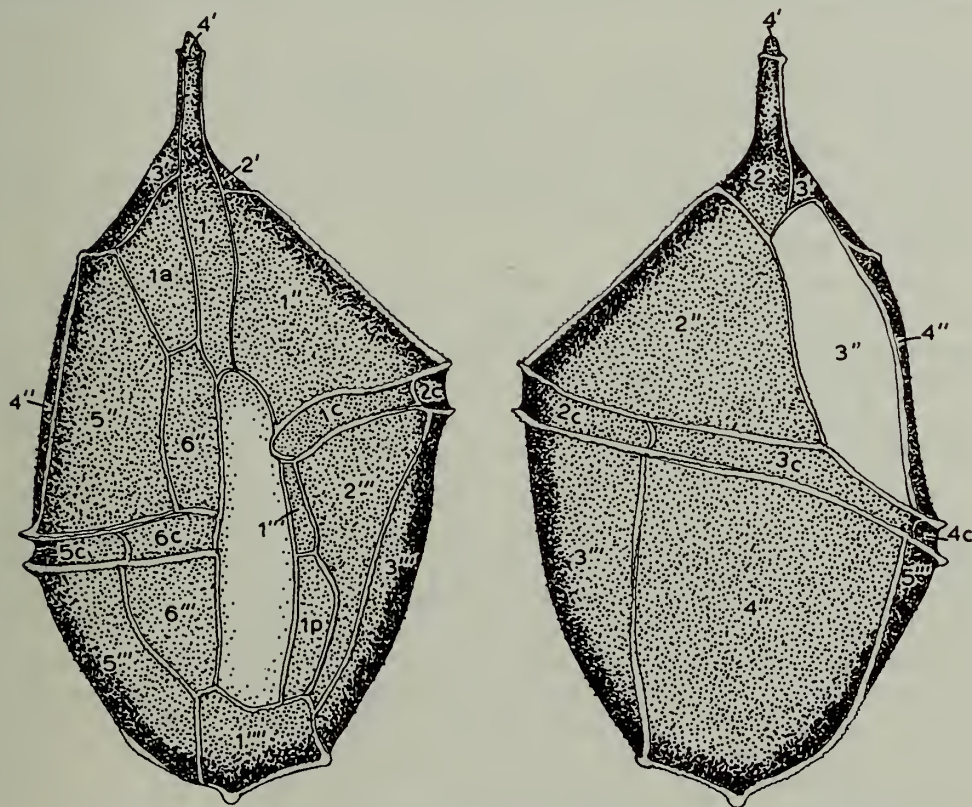


FIG. 30. *Gonyaulacysta aichmetes* sp. nov. Tabulation. Left, ventral view ; right, dorsal view. $\times$ c. 1000.

DIAGNOSIS. A *Gonyaulacysta* with ovoidal to broadly ellipsoidal theca and strong, tapering apical horn accounting for about one-sixth to one-seventh of overall length. Tabulation 4', 1a, 6", 6c, 6''', 1p, 1'''. Crests delimiting plates represented by low ridges, minutely serrate; those bordering cingulum higher. Cingulum strongly spiral, of moderate breadth; sulcus sunken, broad, with only short epitrectal section. Surface of shell densely granular; granulation less pronounced on sulcus.

HOLOTYPE. B.M.(N.H.) slide V.51730(2). Speeton Clay, Shell West Heslerton Borehole No. 1, West Heslerton, Yorks., at 19.25 metres depth. Lower Cretaceous (Upper Barremian).

DIMENSIONS. Holotype: overall length 101μ , breadth 64μ (minimum); shell length 84μ , breadth 56μ (minimum); length of horn, 16μ ; width of cingulum c. 4.5μ . Range of dimensions: overall length c. 95 – 105μ , breadth c. 55 – 65μ .

DESCRIPTION. This is a relatively infrequent species, some 6 specimens only having been studied. The holotype was the best oriented for study, but is somewhat crushed in at right, so that breadth measurements stated are minima and the right-hand tabulation is possibly inaccurate, albeit confirmed in some measure by study of other specimens.

There are four apical plates; the apical horn is tipped by plate 4', its flanks being formed by the other three plates. Plate 1' is especially elongate, extending down almost two-thirds of the epitract. Six precingular plates are present, plate 6" being reduced to accommodate a very large anterior intercalary plate. Six post-cingular plates are present, with plate 1''' reduced and very elongate; an elongate posterior intercalary plate lies between it and the antapex. A single, rather quadrate plate occupies the antapex.

The cingulum forms a strong laevorotatory spiral such that its two ends differ in antero-posterior position by twice its width. It is bordered by strong ridges. The cingular plates are poorly defined, but appear to be six in number. The sulcus is broad and relatively short, extending to the antapex.

The shell surface is densely granular. The crests are low but generally readily perceptible: they are finely but irregularly serrate.

A precingular pylome, formed by loss of plate 3", is present in all specimens seen.

REMARKS. *Gonyaulacysta aichmetes* sp. nov. is of a general form similar to several other Cretaceous species, but is distinguished by shape, crest character and detail of the tabulation. The most comparable species is undoubtedly *Gonyaulacysta apionis* (Cookson & Eisenack 1958) from the Albion of South Australia. However, this latter species has a more ellipsoidal shape, smooth crests and four pronounced projections bordering the antapical plate; its tabulation has not been fully specified, but, from the figures given (Cookson & Eisenack 1958, text-figs. 3, 4) plate 1 appears to be less elongate, there appears to be no anterior intercalary plate, and the posterior ventral structure appears different. The "lid" on the apical horn of *G. apionis* is probably simply a small apical plate edged by crests, such as is present in *G. aichmetes*.

Gonyaulacysta cassidata (Eisenack & Cookson)

Pl. 14, figs. 3, 4 ; Text-fig. 31

1960. *Gonyaulax helicoidea* subsp. *cassidata* Eisenack & Cookson : 3, pl. 1, figs. 5, 6.
 1962. *Gonyaulax cassidata* Eisenack & Cookson ; Cookson & Eisenack : 486, pl. 2, figs. 1, 2.
 1964. *Gonyaulax cassidata* Eisenack & Cookson ; Cookson & Hughes : 42, pl. 5, fig. 10 only.

EMENDED DIAGNOSIS. A *Gonyaulacysta* with thin-walled, broadly ovoidal theca, surmounted by apical pericoel terminating in short horn. Tabulation 4', 1a, 6'', 6c, 6''', 1p, 1'''' ; plate boundaries demarcated by high, delicate crests with smooth or denticulate edges. Cingulum strongly spiral, of moderate breadth : sulcus broadening posteriorly, weakly sigmoidal. (A median dorso-ventral plane would barely intersect the two ends of the cingulum.) Surface of shell smooth or only minutely granular : irregular scatter of tubercles present in some specimens.

HOLOTYPE. Specimen P.17869, National Museum of Victoria, Australia. Lower Cretaceous (Albian) ; Santos's Oodnadatta bore, South Australia, at 327 feet depth.

MATERIAL (figured). Geol. Surv. Colln. slide PF.3047(1). Chalk, H.M. Geological Survey Borehole, Fetcham Mill, Surrey, at 730 feet depth. Upper Cretaceous (Cenomanian).

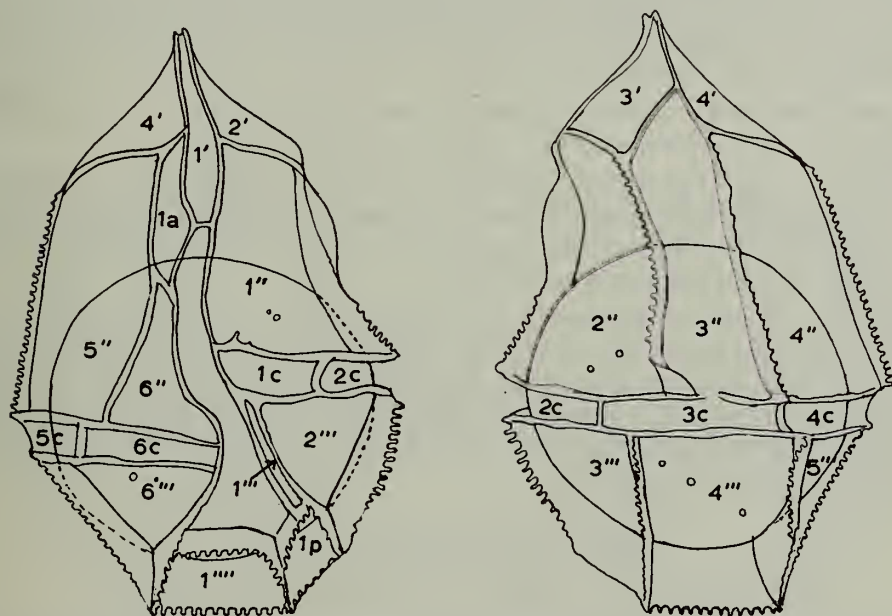


FIG. 31. *Gonyaulacysta cassidata* (Eisenack & Cookson). Tabulation. Left, ventral view ; right, dorsal view. $\times$ c. 1000.

DIMENSIONS. Holotype : overall length 83μ , breadth 52μ . Range of Australian specimens : overall lengths 71 to 95μ , breadths 47 to 57μ . Figured specimen : overall length 78μ , breadth 53μ , shell length 42μ , breadth 45μ . Range of English specimens : overall lengths 60 to 78μ breadths 46 to 53μ .

DESCRIPTION. Shell broadly ovoidal, the apical pericoel and high antapical crests imparting a polygonal appearance. The crests separating the four apical plates converge at the top of the apical horn, which has a bifid appearance. Plate 1' is elongate but relatively short, occupying the anterior prolongation of the sulcus. The apical pericoel comprises the apical plates, the anterior intercalary plate and the anterior portions of the six precingular plates : its volume is between one-third and two-thirds that of the shell proper. The anterior plate is somewhat elongate : plate 6'' is reduced and almost triangular. Six postcingular plates are present. Plate 1''' is reduced and linear, difficult to see in many specimens : it is displaced by the posterior broadening of the sulcus. A small, quadrate posterior intercalary plate separates plates 1''' and 2''' from the single, polygonal antapical plate.

The cingulum forms a laevo-rotatory spiral such that its two ends differ in antero-posterior position by over twice its width. It is composed of six plates. The sulcus is of moderate breadth on the epitract but broadens considerably as it approaches the antapex.

The shell wall and the crests are both delicate. The crests are high, typically but not consistently denticulate, sometimes minutely and irregularly perforate : the very high crests surrounding the antapex appear to be sustained by delicate spines at the angles. Tubercles may be present ; their number and distribution varies considerably between individuals.

A precingular archaeopyle is formed by loss of plate 3'' : in some specimens, including the figured specimen, the cingulum is slightly torn also.

REMARKS. The diagnosis is emended to include reference to the tabulation. The English specimens correspond closely to those figured from Australia, differing only in details of shape and proportionate size of shell and pericoel, features in which some degree of variation would be expected.

Cookson & Hughes (1964) described this species from the Cambridge Greensand (?Albian-basal Cenomanian) : of two forms figured, one (p. 5, fig. 10) corresponds to *Gonyaulacysta cassidata* as here interpreted, the other (p. 5, fig. 11) appears to belong to *Psaligonyaulax deflandrei* sp. nov. (p. 137). Both species range right through the Cenomanian horizons of the Chalk of the Fetcham Mill Borehole, albeit consistently in low numbers only.

***Gonyaulacysta whitei* sp. nov.**

Pl. 14, fig. 2 ; Text-fig. 32

DERIVATION OF NAME. Named in honour of two early workers on fossil microplankton—Henry Hopley White of Clapham, England, an amateur microscopist

who described assemblages from the Chalk in 1842-44, and M. C. White of the United States, who described in 1862 the first Palaeozoic assemblages, from New York State.

DIAGNOSIS. A *Gonyaulacysta* having an ovoidal theca with short, blunt apical horn formed from both shell layers. Tabulation 3', 1a, 6'', 6c, 6''', 1p, 1'''' : plate boundaries demarcated by moderately high crests, densely and finely perforate, with straight or ragged edges. Cingulum broad, strongly spiral : sulcus sigmoidal, of moderate breadth but widening somewhat posteriorly. (A median dorso-ventral plane would barely intersect the two ends of the sulcus.) Surface of shell smooth or only very minutely granular. Crests bounding antapex supported at the angles by strong, broad spines.

HOLOTYPE. Geol. Surv. Colln. slide PF.3048(1), Chalk. H.M. Geological Survey Borehole, Fetcham Mill, Surrey at 770 feet depth. Upper Cretaceous (Cenomanian).

DIMENSIONS. Holotype : overall length 62μ , breadth 49μ : shell length 53μ , breadth 45.5 ; length of horn 9μ .

DESCRIPTION. Shell rotund, lemon-shaped, the apical horn joining the shell so smoothly as to have no precise base. Only three apical plates, the crests bounding them forming a pimple on the tip of the apical horn. Plate 1' is elongate and occupies the anterior prolongation of the sulcus : its posterior boundary was not clearly determined. An anterior intercalary plate and six precingular plates are present, plate 6'' being reduced and subtriangular. Six postcingular plates are present, plate 1''' being very small and having an ill-defined boundary with the sulcus. The single posterior intercalary plate separates plates 1''' and 2''' from the quadrate antapical plate.

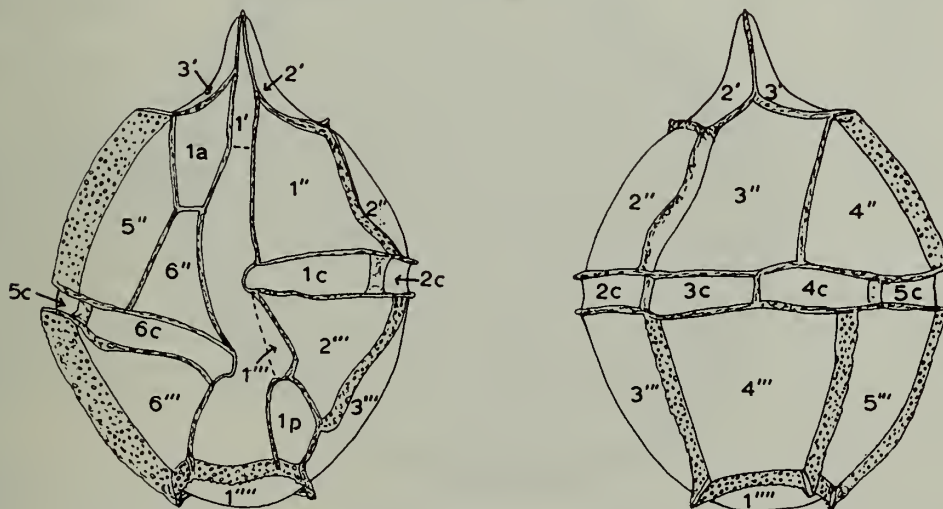


FIG. 32. *Gonyaulacysta whitei* sp. nov. Tabulation. Left, ventral view ; right, dorsal view. $\times$ c. 1000.

The cingulum forms a laevorotatory spiral such that its two ends differ in antero-posterior position by almost 4 times its breadth. Six cingular plates are present: the ends of plates 1c and 6c extend somewhat into the sulcus. The epitracial portion of the sulcus is of moderate breadth; the hypotracial portion broadens progressively as it approaches the antapex.

A precingular archaeopyle is formed by loss of plate 3".

REMARKS. This species is based on a single specimen, well preserved and displayed: its characters are considered sufficiently distinctive to justify creation of a new species. Shape, tabulation and crest character distinguish *Gonyaulacysta whitei* sp. nov. from all other described species.

Gonyaulacysta fetchamensis sp. nov.

Pl. 15, figs. 1, 2; Text-fig. 33

DERIVATION OF NAME. Refers to the type locality, Fetcham Mill, Surrey.

DIAGNOSIS. A *Gonyaulacysta* having an ovoidal theca with strong, blunt apical horn formed by periphragm only. Tabulation 3-24', 1a, 6", 6c, 7"', 2p, 1''''; sutures in form of low but well-marked, rather fibrous crests giving rise occasionally to short, blunt spines. Cingulum narrow, strongly spiral; sulcus broad, sunken. Shell surface densely granular.

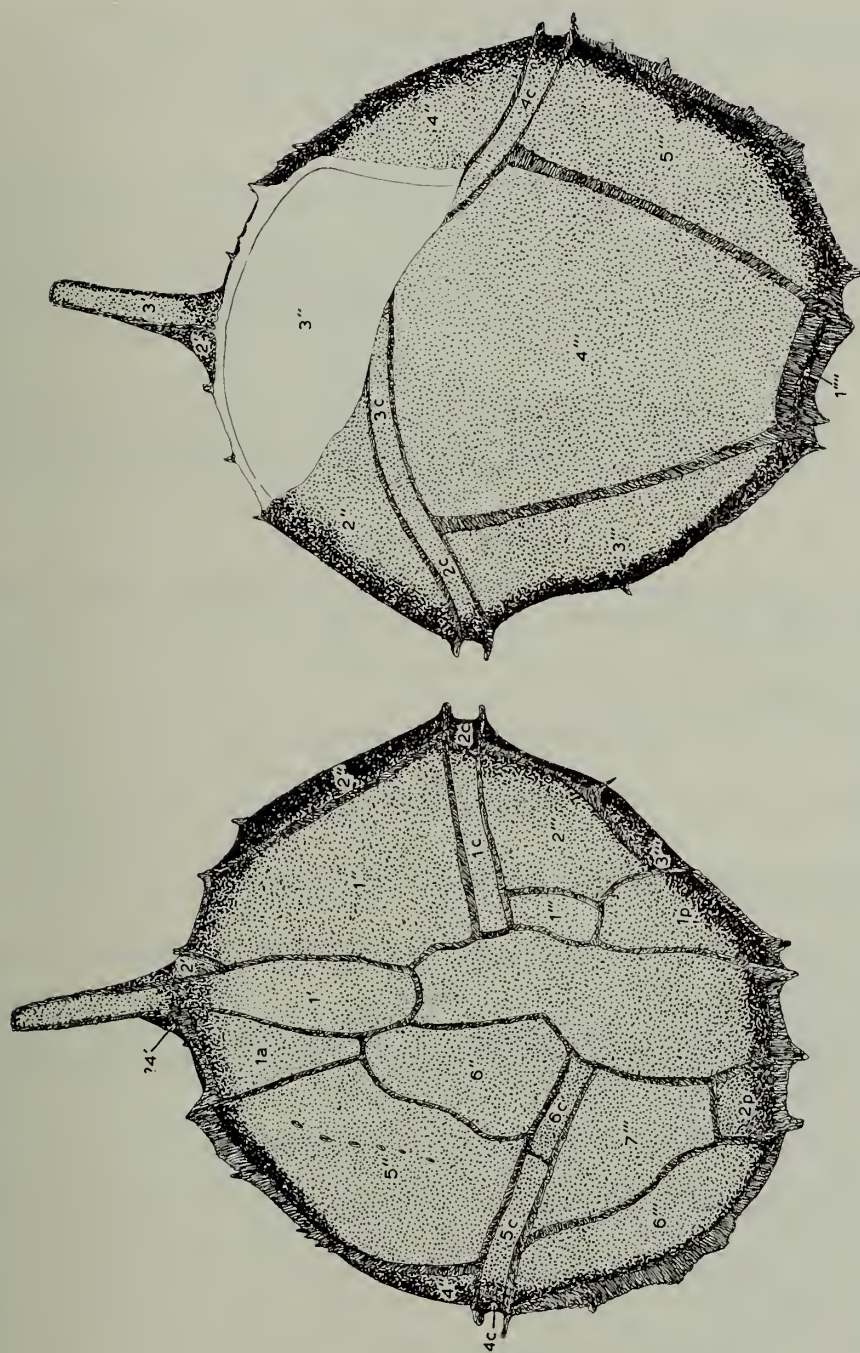
HOLOTYPE. Geol. Surv. Colln. slide PF.3046(1). Chalk, H.M. Geological Survey Borehole, Fetcham Mill, Surrey, at 840 feet depth. Upper Cretaceous (basal Cenomanian).

DIMENSIONS. Holotype: overall length 125 μ , breadth 108 μ ; shell length 95 μ , breadth 98 μ ; length of horn c.25 μ .

DESCRIPTION. This species is extremely infrequent: of three specimens encountered, one (the holotype) is well preserved, the other two are severely damaged.

The shell is broadly ovoidal, giving rise to a strong, blunt apical horn; this horn is formed by the periphragm only and constitutes what is effectively an apical pericoel. There are certainly three and possibly four apical plates, presence of a crest separating plates 3' and 4' being unconfirmed. Plate 1' is unusually large and club-shaped. Six precingular plates are present, with plate 6" reduced to accommodate a sub-triangular anterior intercalary plate. Seven postcingular plates are present. Plates 1'''' and 2'''' are reduced to accommodate a large posterior intercalary plate, and plate 7''' is also reduced to accommodate a second, smaller intercalary plate. (The crest separating plates 5''' and 6''' is somewhat torn.) The antapex is occupied by a single plate of moderate size.

The cingulum is narrow, forming a laevorotatory spiral such that its two ends differ in antero-posterior position by almost three times its width. The ends of the cingulum are widely separated by a very broad sulcus, which widens further in its posterior portion.



The crests are fibrous in nature, with close-set slits in places : they give rise to occasional short spines. In the holotype a broken line of "tubercles", like an embryonic crest, crosses plate 5" ; this was not observed in the other specimens.

A precingular archaeopyle is formed by loss of the large plate 3". In the holotype, the region round the archaeopyle is somewhat folded.

REMARKS. The generic allocation of *Gonyaulacysta fetchamensis* is questionable, in view of its possession of two posterior intercalary plates and a seventh postcingular plate. The similarity in general morphology to a number of Lower Cretaceous species of *Gonyaulacysta* resulted in its allocation to that genus ; however, it may subsequently prove preferable to erect a new genus for species having this tabulation pattern, a procedure not now adopted in view of the low numbers of specimens encountered to date.

The most closely comparable species is undoubtedly *Gonyaulacysta orthoceras* (Eisenack), which has a similar general form and apical horn. However, *Gonyaulax fetchamensis* is clearly distinguished by the form of its crests and the detail of ventral tabulation.

OTHER SPECIES

The following species are here attributed to the genus *Gonyaulacysta* on the basis of general structure and formation of an archaeopyle by loss of plate 3" :

Gonyaulacysta aculeata (Klement 1960). Upper Jurassic (?Oxfordian–Kimmeridgian) ; Germany.

Gonyaulacysta amabilis (Deflandre 1939). Upper Jurassic (Kimmeridgian) ; France.

Gonyaulacysta ambigua (Deflandre 1939). Upper Jurassic (Kimmeridgian) ; France.

Gonyaulacysta apionis (Cookson & Eisenack 1958). Lower Cretaceous (Albian) ; South Australia.

Gonyaulacysta aptiana (Deflandre 1935). Lower Cretaceous (Aptian) ; France (see p. 140).

Gonyaulacysta cladophora (Deflandre 1938). Upper Jurassic (Oxfordian) ; France.

Gonyaulacysta clathrata (Cookson & Eisenack 1960b). Upper Jurassic (?Tithonian) ; Western Australia.

Gonyaulacysta crassicornuta (Klement 1960). Upper Jurassic (Kimmeridgian) ; Germany.

Gonyaulacysta cretacea (Neale & Sarjeant 1960). Lower Cretaceous (Hauterivian) ; England.

Gonyaulacysta diaphanis (Cookson & Eisenack 1958). Cretaceous (?Aptian) ; Western Australia.

Gonyaulacysta edwardsi (Cookson & Eisenack 1958). Cretaceous (Aptian–Turonian) ; Australia.

Gonyaulacysta eisenacki (Deflandre 1938). Upper Jurassic (Oxfordian) ; France.
Gonyaulacysta eumorpha (Cookson & Eisenack 1960b). Upper Jurassic (Oxfordian–Lower Kimmeridgian) ; Western Australia.

Gonyaulacysta granulata (Klement 1960). Upper Jurassic (Oxfordian–Kimmeridgian) ; Germany.

Gonyaulacysta granuligera (Klement 1960). Upper Jurassic (Kimmeridgian) ; Germany.

Gonyaulacysta hyalodermopsis (Cookson & Eisenack 1958). Lower Cretaceous (?Aptian) ; Western Australia.

Gonyaulacysta margaritifera (Cookson & Eisenack 1960a). Upper Cretaceous (Senonian) ; Western Australia.

Gonyaulacysta microceras (Eisenack 1958). Lower Cretaceous (Aptian) ; Germany.

Gonyaulacysta millioudi (Sarjeant 1963b, 1965). Upper Jurassic (Oxfordian) ; Switzerland.

Gonyaulacysta muderongensis (Cookson & Eisenack 1958). Lower Cretaceous (Aptian) ; Western Australia.

Gonyaulacysta obscura (Lejeune-Carpentier 1946). Upper Cretaceous ; Belgium.

Gonyaulacysta pachyderma (Deflandre 1938). Upper Jurassic (Oxfordian) ; France.

Gonyaulacysta perforans (Cookson & Eisenack 1958). Upper Jurassic ; Papua.

Gonyaulacysta scarburghensis Sarjeant 1964b (= *Gonyaulax areolata* n.n. Sarjeant 1961). Upper Jurassic (Oxfordian) ; England.

Gonyaulacysta scotti (Cookson & Eisenack 1958). Upper Jurassic ; Western Australia.

Gonyaulacysta serrata (Cookson & Eisenack 1958). Upper Jurassic–?Lower Cretaceous ; Papua.

Gonyaulacysta tenuiceras (Eisenack 1958). Lower Cretaceous (Aptian) ; Germany.

Gonyaulacysta wetzeli (Lejeune-Carpentier 1939). Upper Cretaceous ; Belgium.

The following described species are doubtfully included in *Gonyaulacysta* on the basis of general structure but in absence of clear knowledge of the mode of archaeopyle formation.

?*Gonyaulacysta aceras* (Eisenack 1958). Lower Cretaceous (Aptian) ; Germany.

?*Gonyaulacysta cornigera* (Valensi 1953). Middle Jurassic (Bathonian) ; France.

?*Gonyaulacysta freakei* (Sarjeant 1963b). Upper Jurassic (Oxfordian) ; England.

?*Gonyaulacysta longicornis* (Downie 1957). Upper Jurassic (Kimmeridgian) ; England.

?*Gonyaulacysta mamillifera* (Deflandre 1939). Upper Jurassic (Kimmeridgian) ; France.

?*Gonyaulacysta nannotrix* (Deflandre 1939). Upper Jurassic (Kimmeridgian) ; France.

?*Gonyaulacysta nealei* (Sarjeant 1962b). Upper Jurassic (Oxfordian) ; England.

?*Gonyaulacysta nuciformis* (Deflandre 1938). Upper Jurassic (Oxfordian) ; France.

?*Gonyaulacysta porosa* (Lejeune-Carpentier 1946). Upper Cretaceous ; Belgium.

?*Gonyaulacysta transparens* (Sarjeant 1959). Middle Jurassic (Callovian) ; England.

Genus *ACANTHOGONYAULAX* nov.

DERIVATION OF NAME. Greek, *akantha*, thorn, prickle ; a spiny variant of the *Gonyaulax* tabulation type.

DIAGNOSIS. Proximate dinoflagellate cysts, spherical, ellipsoidal, ovoidal or polyhedral, with the tabulation 3-4', 0-1a, 6", 6g, 6'''', 1p, 0-1 p.v., 1'''''. Cingulum strongly or weakly helicoid ; sulcus generally or constantly extending on to epitract. Apical horn present only infrequently ; median and antapical horns lacking. Sutures in form of low ridges bearing rows of spines, simple or furcate, or distinguishable only as rows of spines. Shell bearing general cover of simple or furcate spines, identical to or differing from those on sutures ; spines fewer or totally lacking on cingulum and/or sulcus. Length of spines always less than $\frac{1}{4}$ of shell width. Surface smooth, granular, nodose, punctate or reticulate. Precingular archaeopyle formed by loss of plate 3".

TYPE SPECIES. *Gonyaulax venusta* Klement 1960. Upper Jurassic (Oxfordian to Kimmeridgian) ; Germany.

REMARKS. There are a group of Upper Jurassic species characterized by possession of a dense spine cover, through which a tabulation of *Gonyaulax* type may be determined with varying degrees of difficulty. It is probable that these forms developed into spinous species without tabulation. These species form a coherent group which are considered to merit a separate generic name. *Gonyaulax venusta* is selected as type-species, since it shows the tabulation most clearly.

Forms of *Gonyaulacysta* with a coarsely tubercular surface, such as *G. aculeata* (Klement 1960) may represent a transitional stage to *Acanthogonyaulax*.

The following species accord with the diagnosis of this genus :

Acanthogonyaulax acanthosphaera (Sarjeant 1961) comb. nov., Upper Jurassic (Oxfordian) ; England.

A. paliuros (Sarjeant 1962a) comb. nov. Upper Jurassic (Oxfordian) ; England.

Genus *HESLERTONIA* nov.

DERIVATION OF NAME. Based on the name West Heslerton, Yorkshire, from which the type species was first described.

DIAGNOSIS. Chorate dinoflagellate cysts, spherical, ellipsoidal, ovoidal or polyhedral, with high sutural crests outlining the tabulation 3-4', 0-1a, 6'', 6g, 6''', 1p, 0-1 p.v., 1'''. Cingulum strongly or weakly helicoid; sulcus generally but not constantly extending on to epitract. Apical and antapical horns absent. Sutures perforate or imperforate; their distal edges smooth or denticulate. Crest height exceeds $\frac{1}{4}$ of shell width. Surface smooth, granular, punctate, nodose or reticulate. Precingular archaeopyle formed by loss of plate 3''; archaeopyle sometimes absent.

TYPE SPECIES. *Gonyaulax heslertonense* Neale & Sarjeant 1962. Lower Cretaceous (Hauterivian); England.

REMARKS. This genus is a chorate equivalent of *Gonyaulacysta*, characterized by its disproportionately high crests.

Heslertonia heslertonensis (Neale & Sarjeant)

1962. *Gonyaulax heslertonense* Neale & Sarjeant: 440, pl. 19, fig. 5, pl. 20, fig. 5; text-fig. 1.

REMARKS. Forms closely comparable to this species have been figured and described from the Middle Cretaceous of Australia as *Cymatiosphaera striata* Eisenack & Cookson (1960: 9, pl. 3, figs. 10, 11). Both forms have in common high, striate crests: the figures suggest that the Australian species also has a cingulum and a determinable tabulation. A full restudy of the Australian specimens appears necessary to determine whether *H. heslertonense* and *C. striata* are congeneric or conspecific; should the latter prove to be the case, the earlier name *striata* would have priority.

Genus *LEPTODINIUM* Klement 1960: 45

EMENDED DIAGNOSIS. Proximate dinoflagellate cysts, spherical, ovoidal, ellipsoidal or polyhedral, with the tabulation 4', 6'', 5-?6g, 5''', 1p, 1'''. Cingulum strongly or weakly helicoid, sulcus generally but not constantly extending on to epitract, undivided or subdivided into a pattern of ventral plates. Sutures between plates in form of low ridges, or bearing crests of varied form (smooth, denticulate or spinous; perforate or imperforate). Height of crests always less than $\frac{1}{4}$ of shell width. Surface of shell smooth, granular or punctate. Precingular archaeopyle formed by loss of plate 3''; not all individuals may show an archaeopyle.

TYPE SPECIES. *Leptodinium subtile* Klement 1960. Upper Jurassic (Oxfordian to Lower Kimmeridgian); Germany.

REMARKS. The diagnosis is emended to include mention of the archaeopyle and more detail of other features. Differentiating features from *Gonyaulacysta* are the smaller number of postcingular plates and the lack of an anterior intercalary plate. A number of species of the latter genus show reduction of the first post-ingular plate : presence or absence of an anterior intercalary plate is then determinative.

Leptodinium alectrolophum sp. nov.

Pl. 15, figs. 3-6 ; Text-fig. 34

DERIVATION OF NAME. Greek, *alectrolophos*, cockscomb, in reference to the distinctive crests.

DIAGNOSIS. A *Leptodinium* having an ovoidal theca, without apical horn. Tabulation 4', 6'', 7c, 5''', 1p, 1'''' ; plate boundaries bearing high, delicate crests which form slight projections at their points of junction. Sulcus and cingulum both of moderate breadth : sulcus relatively long, extending almost from apex to antapex. Cingular plate 7c roughly diamond-shaped. Apical prominence formed by junction of crests of apical plates.

HOLOTYPE. B.M.(N.H.) slide V.51725(1). Speeton Clay, Shell West Heselton Borehole No. 1., West Heselton, Yorks., at 39 metres depth. Lower Cretaceous (Middle Barremian).

PARATYPE. V.51725(2). Same locality and horizon.

DIMENSIONS. Holotype : overall length 56μ , breadth 50μ ; shell length 47.5μ , breadth 42.5μ ; width of cingulum $c.5.5\mu$. Paratype : overall length 61.5μ , breadth 54.5μ ; shell length 50μ , breadth 46μ ; width of cingulum $c.6\mu$. Other specimens observed were of intermediate dimensions.

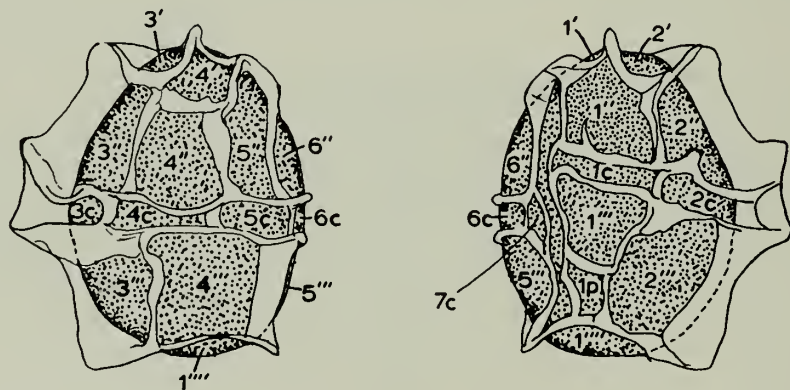


FIG. 34. *Leptodinium alectrolophum* sp. nov. Tabulation. Left, oblique dorsal view ; right, oblique ventral view. $\times c. 800$.

DESCRIPTION. Theca ovoidal, an appearance of polygonality being imparted by the crests. The pericoel surface bears a coarse granulation, granules being rather regularly spaced. The crests are thin and high, with minute, inconspicuous perforations. Their distal edge is usually smooth, occasionally finely denticulate ; crests of a single individual may in part have smooth, in part denticulate, edges.

The apical prominence appears to be formed solely by the junction of crests bounding the four apical plates ; there appears to be no apical horn as such. Apical plate 1' occupies the anterior extension of the sulcus ; since the sulcus is long and approaches the apex, plate 1' is proportionately small. The six precingular plates are all quite large. Presence of an anterior intercalary plate was suspected but not confirmed ; if present, this plate is relatively small. Five well-developed postcingular plates are present ; plate 1''' is reduced to accommodate a quadrate posterior intercalary plate. The antapex is occupied by a single, large plate.

The cingulum forms a strong laevorotatory spiral such that its two ends differ in antero-posterior position by roughly twice its width. There are six clear cingular plates, plus a seventh, diamond-shaped plate, here designated 7c, which lies between the posterior end of the cingulum and the sulcus. The sulcus is narrow and long, extending almost from apex to antapex.

An archaeopyle is not present in the holotype ; however, the paratype has a well-developed precingular archaeopyle formed by loss of plate 3''.

REMARKS. *Leptodinium alectrolophum* differs from all described species in its combination of crest and thecal morphology and tabulation. It resembles *Gonyaulacysta gongylos* in having a seventh polygonal plate at the posterior end of the cingulum, but differs in tabulation and crest form and shape. *Heslertonia heslertonense* has even higher crests ; the surface lacks similar granulation and the tabulation is again different.

In certain orientations, the high crests of this species produce a misleading resemblance to *Scriniodinium* ; however, detailed study shows that no pericoel is present.

The form from the Aptian of Germany, figured by Eisenack (1958, pl. 22, fig. 4) as ?*Gonyaulax* sp., may well be attributable to this species.

Presence of only five postcingular plates presumably results from the trend of reduction of plate 1''' ; thus plate 1''' of *Leptodinium* corresponds to plate 2''' of *Gonyaulacysta*.

OTHER SPECIES

The following species are retained in this genus and accord with the emended diagnosis :

Leptodinium arcuatum Klement 1960. Upper Jurassic (Upper Oxfordian) ; Germany.

Leptodinium maculatum Cookson & Eisenack 1961b. Eocene ; Rottneest Island, Western Australia.

Leptodinium membranigerum Gerlach 1961. Oligocene ; Germany.

Leptodinium mirabile Klement 1960. Upper Jurassic (?Oxfordian-Lower Kimmeridgian) ; Germany.

?*Leptodinium tenuicornutum* Cookson & Eisenack 1962b. Cretaceous (?Albian) ; Western Australia.

Genus **RAPHIDODINIUM** Deflandre 1936 : 184

TYPE SPECIES. *Raphidodinium fucatum* Deflandre 1936. Upper Cretaceous ; France.

REMARKS. This genus comprises highly condensed proximo-chorate cysts of ovoidal shape, characterized by possession of a very few extremely long spines, about 12 in number and up to twice the shell length. The shell surface bears low crests outlining a tabulation : the spines arise from crest nodes. The tabulation has not been determined, nor has an archaeopyle been reported ; the systematic position thus remains obscure. It is clearly a cyst genus, however, since spines arise from the cingulum.

Genus **PSALIGONYAULAX** nov.

DERIVATION OF NAME. Greek, *psalis*, low building with a vaulted roof ; a variant of the *Gonyaulax* tabulation type with terminal pericoels.

DIAGNOSIS. Bicavate dinoflagellate cysts, pericoel separated into two portions by broad median zone of contact with inner body. Outline spheroidal to ellipsoidal or subpolygonal with apical horn. Tabulation 3-4', 1a, 6", 6c, 6'''', 1p, 1'''' determinable on periphragm, sutures in form of ridges of varied height and ornament. No spines arise from crest nodes. Surface of endophragm and periphragm smooth, granular, nodose, reticulate or punctate. Precingular archaeopyle formed by loss of plate 3".

TYPE SPECIES. *Psaligonyaulax deflandrei* sp. nov. Upper Cretaceous (Cenomanian) ; England.

REMARKS. This new genus is distinguished from *Gonyaulacysta* by the presence of apical and antapical pericoels ; the species *Gonyaulacysta cassidata*, which has a closely similar tabulation pattern to that of the type species of *Psaligonyaulax* and which has an apical pericoel but no antapical pericoel, may well represent an intermediate form.

Psaligonyaulax is distinguished from *Scriniodinium* sensu stricto by the separation of the pericoel into two parts ; from the subgenus *Scriniodinium* by the presence of a clear tabulation ; from the subgenus *Endoscrinium* by possession of a posterior intercalary plate and an antapical plate.

Psaligonyaulax deflandrei sp. nov.

Pl. 14, figs. 7, 8 ; Text-fig. 35

1964. *Gonyaulax cassidata* Eisenack & Cookson ; Cookson & Hughes : 42, pl. 5, fig. 11 only.

DERIVATION OF NAME. Named in honour of Professor Georges Deflandre, who has published fundamental studies of dinoflagellates in the French Upper Cretaceous between 1932 and the present.

DIAGNOSIS. A *Psaligonyaulax* having a spindle-shaped outline, truncated posteriorly, with ovoidal inner body. Apical pericoel surmounted by bifid horn, antapical pericoel flattened. Tabulation 4', 1a, 6'', 6c, 6''', 1p, 1'''''. Crests of moderate height with smooth or denticulate edges. Cingulum broad, strongly spiral : sulcus narrower but widening posteriorly. Surfaces of endophragm and periphragm smooth or only minutely granular : an irregular scatter of tubercles may be present on periphragm.

HOLOTYPE. Geol. Surv. Colln. slide PF.3049(1). Chalk, H.M. Geological Survey Borehole, Fetcham Mill, Surrey, at 730 feet depth. Upper Cretaceous (Cenomanian).

DIMENSIONS. Holotype : overall length 75μ , breadth 44μ ; length of inner body 35μ , breadth 40μ . Range of dimensions : overall lengths 72 to 82μ , breadths 43 to 60μ .

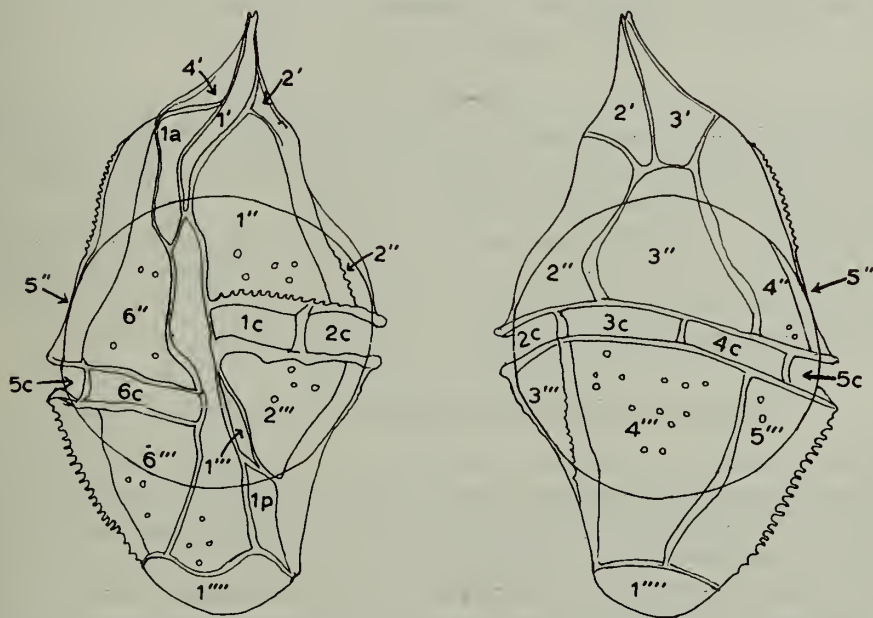


FIG. 35. *Psaligonyaulax deflandrei* sp. nov. Tabulation. Left, ventral view ; right, dorsal view (plate 3'' is missing). $\times$ c. 1000.

DESCRIPTION. The apical horn is more or less conical, a bifid appearance being imparted by the apical junction of crests separating the four apical plates. Plate 1' is narrow and elongate, occupying the anterior prolongation of the sulcus; the anterior intercalary plate is also rather elongate. Six precingular and six postcingular plates are present: plate 1''' is very reduced and elongate. A posterior intercalary plate separates plates 1''' and 2''' from the single plate occupying the antapex.

The cingulum forms a laevorotatory spiral such that its two ends differ in antero-posterior position by three times its width: six cingular plates are present. The sulcus is constricted in its median portion, but widens considerably as it approaches the antapex.

The crests are in part smooth, in part denticulate: they are sometimes very finely perforate. A scatter of tubercles may be present, their number and distribution varying considerably between individuals.

Plate 3" is consistently lost in archaeopyle formation: its absence is not always obvious in unstained specimens, as a result of the delicacy and transparency of the shell.

REMARKS. *Psaligonyaulax deflandrei* sp. nov. is present throughout the Cenomanian of the Fetcham Mill Borehole, but it is never abundant. Cookson & Hughes (1964) figured a representative of this species from the Cambridge Greensand (?Albian-Cenomanian) as *Gonyaulax cassidata*. The latter species, now *Gonyaulaesytia cassidata*, has a comparable distribution and a similar tabulation: it may be related to *P. deflandrei*, but intermediate forms are not known.

OTHER SPECIES

The species *Scriniodinium apaletum* Cookson & Eisenack 1960, from the Upper Jurassic of Australia and Papua, appears attributable to *Psaligonyaulax*: its tabulation has not, however, been described to date.

Following the reconsideration herein of the genera *Hystrichosphaeropsis* and *Rottnestia*, the species *R. simplicia* Cookson & Eisenack 1961b, which has poorly developed apical and antapical pericoels and lacks spines arising from crest nodes, becomes *Psaligonyaulax simplicia* (Tertiary; Rottnest Island, Australia).

Genus *HYSTRICHOSPHEROPSIS* Deflandre 1935

EMENDED DIAGNOSIS. Bicavate dinoflagellate cysts, pericoel divided by broad median zone of contact with inner body. Outline typically somewhat angular, apical and antapical pericoels typically quadrate in outline; apical horn arising from former. Tabulation ?3-4', ?1a, 6", 6c, 6''', 1p, 1''', determinable on periphragm; sutures in form of ridges of varied height and ornamentation; simple or furcate spines of varied length arising from some or all crest nodes. Surface of endophragm and periphragm smooth, granular, punctate, nodose or reticulate. Precingular archaeopyle formed by loss of plate 3".

TYPE SPECIES. *Hystrichosphaeropsis ovum* Deflandre 1935. Upper Cretaceous ; France.

REMARKS. The name *Hystrichosphaeropsis* was originally proposed as a separate genus, but was later relegated to the status of a subgenus of *Hystrichosphaera* (Deflandre 1936b). Its status as a separate genus was implicitly revived by the inclusion of this name in a list of valid genera by Eisenack (1963a : 118).

The generic name *Rottnestia* was subsequently proposed by Cookson & Eisenack (1961b : 40-42). Deflandre, in a letter to the author (written in 1963 and here quoted by permission) comments as follows :

“ Le genre *Rottnestia* Cookson et Eisenack 1961 est synonyme du genre *Hystrichosphaeropsis* Defl. 1935 (subgen. in Defl. 1937). Le type (*H. borussica* Eisenack) est tout à fait semblable à *H. ovum* Defl. 1935. Les autres espèces d'*Hystrichosphaeropsis* sont *H. simplicia* (C. et E.) et *H. wetzeli* ; Defl. 1935.”

On this basis, it appears necessary that the generic name *Rottnestia* should be abandoned. The revised diagnosis of *Hystrichosphaeropsis*, here formulated, incorporates in general the diagnostic features quoted in both earlier diagnoses (i.e. of *Hystrichosphaeropsis* and *Rottnestia*) ; but forms lacking nodal processes are excluded and attributed to the new genus *Psaligonyaulax*. The author was courteously permitted by Prof. Deflandre to examine the type species during a visit to Paris in 1961 ; the tabulation was elucidated to be as here quoted. The figures of *Rottnestia* suggest the same tabulation.

OTHER SPECIES

Although Prof. Deflandre considers *Rottnestia borussica* to be probably conspecific with *Hystrichosphaeropsis ovum*, this remains to be confirmed : the former species is thus provisionally retained as *Hystrichosphaeropsis borussica* (Tertiary ; Rottnest Island, Australia).

Hystrichosphaeropsis wetzeli Deflandre 1935 (Upper Cretaceous ; France) accords with the revised diagnosis.

Genus **CARPODINIUM** Cookson & Eisenack 1962b : 489

TYPE SPECIES. *C. granulatum* Cookson & Eisenack 1962b. Lower Cretaceous (Aptian-Albian) ; Australia.

REMARKS. This genus was diagnosed in the following terms (1962b : 489) :

“ Shell elongate—oval to ellipsoidal, divided almost equally by an equatorial girdle. Epitheca with a distinct horn, hypotheca devoid of horns or projections. Pre- and post-equatorial plates probably six in number, elongate trapezoidal and bordered with wings. The longitudinal furrow broadens gradually from the apex to the antapex. A pylome develops on the dorsal surface of the epitheca.”

In absence of full knowledge of the tabulation, the above diagnosis includes no characters, save possibly the posterior widening of the sulcus, which distinguish it from *Gonyaulax*, as accepted at the time of publication, or from *Gonyaulacysta* as defined by Deflandre and here redefined. The status of this genus must be regarded as questionable.

[Genus **RHYNCHODINIOPSIS** Deflandre 1935]

TYPE SPECIES. *Rhynchodiniopsis aptiana* Deflandre 1935. Lower Cretaceous (Aptian) ; France.

REMARKS. In his first full description of this genus (1936a : 32), Deflandre remarks on its apparent close relationship to *Gonyaulax*. Examination of his excellent figures suggests the tabulation 4-?5', ?1a, 6", 6g, 6"', 1p, 1'''' ; a pre-cingular archaeopyle is present, formed by loss of plate 3". Three distinguishing characteristics are cited by Deflandre—the presence of a strong, hollow, apical horn ; the presence of denticulate, aliform crests on sutures ; and the presence of strong curved spines arising from crest nodes along the edges of the cingulum. The first two characters are shared by many species of *Gonyaulacysta* ; the figures indeed strongly suggest a close affinity to *Gonyaulacysta jurassica*. The third distinguishing character does not alone warrant separation to generic level.

It is considered that this genus was, at the time of its publication, effectively a junior homonym of *Gonyaulax*, none of the characters cited warranting the creation of a new name. It is therefore proposed that the name *Rhynchodiniopsis* be abandoned and the single species, *R. aptiana*, from the Lower Cretaceous (Aptian) of France, be transferred to *Gonyaulacysta*.

Genus **HYSTRICHODINIUM** Deflandre 1935 : 229

EMENDED DIAGNOSIS. Proximo-chorate dinoflagellate cysts, spheroidal, ovoidal or polygonal in shape. Tabulation in general accord with *Gonyaulax* pattern, but not determined in detail. Long, hollow spines, rounded in cross-section and fairly stiff, arising from positions of plate boundaries : plate boundaries otherwise marked by low crests or not at all. Cingulum strongly or weakly helicoid, well-marked ; sulcus poorly marked. Length of spines variable, but typically exceeding $\frac{1}{2}$ of shell width. Shell surface smooth, granular, punctate, nodose or areolate. A pre-cingular archaeopyle formed, presumably by loss of plate 3".

TYPE SPECIES. *Hystrichodinium pulchrum* Deflandre 1935. Upper Cretaceous ; France.

REMARKS. The generic diagnosis is emended to include reference to mode of archaeopyle formation and to specify the correspondence of spine position to sutures. This revision follows the examination of specimens of the type species preserved in flint (see below). The genus as now redefined differs from *Gonyaulacysta* in the height of sutural spines; from *Xiphophoridium* in mode of archaeopyle formation; and from *Heliodinium* in the rounded, not flattened, nature of the spines and the less well-marked sutures.

***Hystrichodinium pulchrum* Deflandre**

Pl. 16, figs. 7, 8

1935. *Hystrichodinium pulchrum* Deflandre : 229, pl. 5, fig. 1; text-figs. 9–11.
 1936a. *Hystrichodinium pulchrum* Deflandre; Deflandre : 58, text-fig. 101.
 1936b. *Hystrichodinium pulchrum* Deflandre; Deflandre : 34, pl. 8, figs. 3–8, pl. 9, fig. 3.
 1941. Dinoflagellate W. Wetzel, O. Wetzel & Deflandre, text-fig. 7.
 1944. *Hystrichodinium pulchrum* Deflandre; de Wit, unnumbered text-fig.
 1952a. *Hystrichodinium pulchrum* Deflandre; Deflandre, text-fig. 103.
 1952b. *Hystrichodinium pulchrum* Deflandre; Deflandre, text-fig. 300B.
 1955. *Hystrichodinium pulchrum* Deflandre; Valensi : 591, pl. 3, fig. 11.
 1959. *Hystrichodinium pulchrum* Deflandre; Gocht : 58, pl. 3, figs. 11a, b, pl. 5, fig. 7.
 1961. *Hystrichodinium pulchrum* Deflandre; Alberti : 14, pl. 8, figs. 6–10.
 1963. *Hystrichodinium pulchrum* Deflandre; Górka : 32, pl. 5, fig. 5.

MATERIAL (Figured). B.M.(N.H.) slide V.13937 (1, 2). Flint from the Chalk (no locality or horizon).

DIMENSIONS. Figured specimens : No. 1 : overall length 102 μ , breadth 98 μ , shell length 55 μ , breadth 44 μ . No. 2 : overall length 115 μ , breadth 80 μ ; shell length 55 μ , breadth 35 μ . Observed range; overall lengths 102–115 μ , breadths 80–101 μ .

REMARKS. This species has long been known from the Upper Cretaceous flints, although its structure has not yet been fully determined. It appears to be synonymous with the species described by White (1842 : pl. 4 div. 3 fig. 6; 1844, pl. 8, fig. 5) and by Wilkinson (1846, pl. 8, figs. 2–3) as *Xanthidium spinosum*; this species was subsequently transferred to *Hystrichosphaeridium* by Deflandre (1937a : 31) and to *Baltisphaeridium* by Downie & Sarjeant (1963 : 92) on taxonomic grounds, but has never been redescribed. Prolonged enquiry by the present author among the universities, libraries and museums of Britain indicates that the holotypes of White and Wilkinson are lost; since *Hystrichodinium pulchrum* is well-defined and a name in widespread use, it is proposed that the earlier name *spinosum* be abandoned.

The above enquiry brought to light a number of unlocalized flint slides, in each case of unspecified source, which contain specimens of “xanthidia”, including a number of examples of *Hystrichodinium pulchrum*. Examination of these indicated the precingular character of the pylome and that the distribution of spines corresponds to the positions of sutures, necessitating revision of the generic diagnosis. A full restudy and redescription of this species, based on material extracted by chemical techniques, is clearly necessary.

OTHER SPECIES

The following species are here attributed to the genus *Hystrichodinium* and accord with the revised diagnosis :

Hystrichodinium compactum Alberti 1961. Lower Cretaceous (Valanginian) ; Germany.

Hystrichodinium furcatum Alberti 1961. Lower Cretaceous (Hauterivian) ; Germany.

Hystrichodinium oligacanthum Deflandre & Cookson 1955. Lower Cretaceous ; Australia.

Hystrichodinium ramoides Alberti 1961. Lower Cretaceous (Barremian) ; Germany.

The two remaining species previously attributed to this genus are considered only doubtfully referable to the revised genus. *?Hystrichodinium amphiacanthum* Cookson & Eisenack 1958, has appendages which are polar in position and may warrant erection as a new genus. *?H. parvum* Alberti 1961, from the Lower Cretaceous (Aptian) of Germany, remains of uncertain generic allocation and merits a full restudy.

Genus *HELIODINIUM* Alberti 1961 : 33

EMENDED DIAGNOSIS. Proximo-chorate dinoflagellate cysts, spheroidal, ovoidal or subpolygonal in shape, with tabulation ?3', ?oa, 6", ?oc, 6''', ?op, 1'''. Sutures faintly marked by ridges or low crests, from which arise flattened, dagger to ribbon-like, very flexible processes ; processes typically simple, bifurcate or multi-furcate. Cingulum strongly or weakly helicoid, bounded by low crests : sulcus less well marked. Shell surface smooth, granular or punctate. Precingular archaeopyle formed by loss of plate 3".

TYPE SPECIES. *Heliodinium voighti* Alberti 1961. Lower Cretaceous (Barremian) ; Germany.

REMARKS. The generic diagnosis is emended to incorporate fuller reference to the tabulation and to include reference to the mode of archaeopyle formation. *Heliodinium* is distinguished from *Hystrichodinium* on the character of its processes.

Heliodinium voighti Alberti

Pl. 16, fig. 2 ; Text-fig. 36

1961. *Heliodinium voighti* Alberti : 33, pl. 8, figs. 1-5.

EMENDED DIAGNOSIS. A *Heliodinium* having a subpolygonal shell, epittract almost conical and hypottract in form of truncated cone. Tabulation ?3', ?oa, 6", ?oc, 6''', ?op, 1'''; sutures generally marked only by low ridges, but cingulum and antapex bordered by low crests. Processes dagger-like, frequently highly folded, length less than half shell length ; distal ends of processes typically simple, rarely bifurcate or trifurcate. Shell surface smooth or only minutely granular.

HOLOTYPE. Preparation No. A26, Geologisches Institut der Universität, Tübingen, Germany. Lower Cretaceous (Upper Barremian) ; Haverlahwiese, Germany.

MATERIAL (figured). Geol. Surv. Colln. slide PF.3035(4). Chalk, H. M. Geological Survey Borehole, Fetcham Mill, Surrey, at 840 feet depth. Upper Cretaceous (basal Cenomanian).

DIMENSIONS. Holotype : shell length 48μ , breadth 38μ , length of processes $16-22\mu$. Range of German specimens : shell length $48-60\mu$, breadth $38-56\mu$, length of processes $16-36\mu$. Specimen here figured : overall length $c.125\mu$, breadth $c.105\mu$: shell length 62μ , breadth 45μ .

DESCRIPTION. This species occurs in low numbers in the assemblages from the Chalk at 840 and 810 feet depth (basal Cenomanian) in the Fetcham Mill bore. Although a number of specimens were available for study, the majority proved unsuitable as a result of distortion or unfortunate orientation : the figured specimen was the only one capable of full study. It was thus not possible to confirm details of the apical structure.

Plate 1' is elongate and corresponds to the apical prolongation of the sulcus. At least two other apical plates appear to be present : no anterior intercalary plate could be distinguished. Six precingular and six postcingular plates are present ; no posterior intercalary plate was distinguished. The antapex is occupied by a single plate.

The cingulum forms a strong laevorotatory spiral whose two ends differ in antero-posterior position by three times its width. There appears to be no separation into cingular plates. The sulcus is narrow and extends to the antapex.

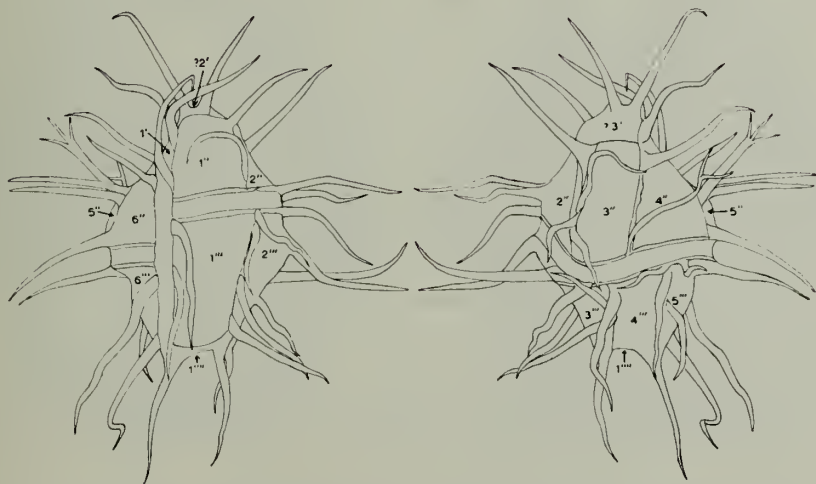


FIG. 36. *Heliodinium voighti* Alberti. Tabulation. Left, ventral view ; right, dorsal view (plate 3'' is missing). $\times c. 500$.

The shell surface appears devoid of ornamentation. The processes are flattened and very flexible, generally simple—one process in the figured specimen is bifurcate, one trifurcate.

Plate 3" is generally lost in pylome formation.

REMARKS. The diagnosis of this species is emended to incorporate new observations. Alberti (1961 : 33) noted the presence of an archaeopyle in one specimen, but did not refer to this in the diagnosis.

The stratigraphic range of the German specimens is Lower Barremian to ?Lower Aptian : the English occurrence thus represents a vertical extension of this range.

***Heliodinium patriciae* Neale & Sarjeant**

Pl. 16, fig. 1

1961. *Heliodinium patriciae* Neale & Sarjeant : 451, pl. 19, fig. 3 ; text-fig. 7.

REMARKS. Re-examination of the holotype (B.M.(N.H.) slide V.51710), and other specimens, suggests a similar tabulation to that of *H. voighti* ; the mode of archaeopyle formation was not determined. In the original text fig. 7, the number of processes shown arising from the cingulum margins is now considered to be somewhat exaggerated ; the figure is correct in all other particulars.

B. Genera with apical archaeopyle

Genus ***MEIOUROGONYAULAX*** nov.

DERIVATION OF NAME. Greek, *meiouro*s, curtailed, shortened ; a variant of the *Gonyaulax* tabulation type shortened by loss of the apex in archaeopyle formation.

DIAGNOSIS. Proximate dinoflagellate cysts, spherical, ellipsoidal, ovoidal or polyhedral, with the tabulation, 4', 0-1a, 6", 6g, 5-6''', 0-1p, 0-1 p.v., 1'''' . Cingulum strongly or weakly helicoid ; sulcus generally or constantly extending on to epitract. Sutures in form of low ridges or bearing crests of varied form (smooth, denticulate or spinous ; perforate or imperforate). Height of crests always less than $\frac{1}{4}$ of shell width. Surface smooth, granular, nodose, punctate or reticulate. Archaeopyle formed by loss of apical plates, part of plate 1' sometimes left attached to shell ; not all individuals show an archaeopyle.

TYPE SPECIES. *Meiourogonyaulax valensii* sp. nov., Middle Jurassic.

REMARKS. This genus presently contains a small group of Jurassic species ; unpublished data available to the author suggests the probability that a number of additional species will be described in the future from the Lower and Middle Jurassic.

The apex has in no case been satisfactorily seen in position. The number of apical plates is deduced from the irregular profile of the archaeopyle and may be subject to future correction.

Meiourogonyaulax valensii sp. nov.

Pl. 15, fig. 7 ; Text-fig. 37

1953. *Gonyaulax* sp. indet., Valensi : 27, pl. 2, figs. 12, 13.

DERIVATION OF NAME. Named after Lionel Valensi, who published the first full descriptions of Middle Jurassic dinoflagellate/acritarch assemblages.

DIAGNOSIS. A *Meiourogonyaulax* having a broadly ellipsoidal theca ; lacking apex in all specimens seen. Tabulation ?4', oa, 6'', 6c, 6''', 1p, 1 p.v., 1'''''. Crests of moderate height, slightly striated and irregularly perforate, with smooth or finely denticulate distal edges. Spines present at some crest nodes. Cingulum strongly spiral, relatively broad ; sulcus broadening posteriorly, subdivided by low ridges. Shell surface punctate or alveolar.

HOLOTYPE. Specimen B.S.60 (L. Valensi preparation), Laboratoire de Micropaléontologie, École Pratique des Hautes Études, Paris. Chert from Airvault, Poitou, France. Middle Jurassic (Bathonian).

DIMENSIONS. Holotype : overall length 70 μ , breadth 70 μ ; shell length, approx. 60 μ , breadth approx. 50 μ ; width of transverse furrow c.6 μ .

DESCRIPTION. Although this species is based on Valensi's single specimen, the author has also seen a number of specimens in material from the Bathonian of the Aquitaine Basin, unfortunately not available for description.

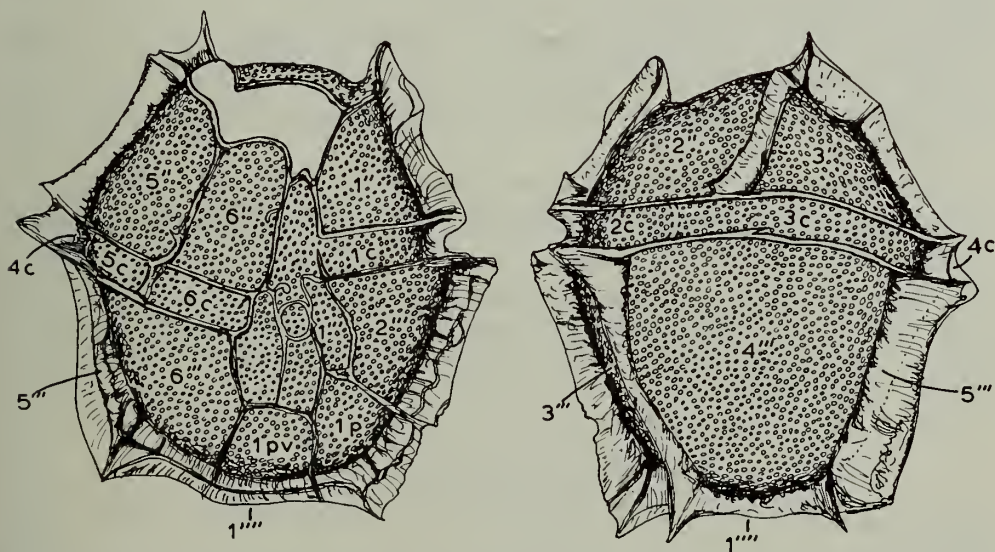


FIG. 37. *Meiourogonyaulax valensii* sp. nov. Tabulation. Left, ventral view ; right, dorsal view. $\times$ c. 1000.

From the angular profile of the apical archaeopyle, the former presence of at least four apical plates is deduced. There is no anterior intercalary plate. Six precingular plates are present, plate 6" being slightly reduced. Six postcingular plates are present, plate 1''' being reduced and elongate, separated from the antapex by a moderately large posterior intercalary plate. The antapex is occupied by a single large plate and is separated from the sulcus by a quadrate posterior ventral plate.

The cingulum forms a strong laevorotatory spiral such that its two ends differ in antero-posterior position by over twice its width. It is clearly subdivided into six cingular plates. The sulcus is roughly wedge-shaped, broadening towards the posterior ; it bears low ridges forming an irregular pattern.

The shell surface is alveolar to punctate. The crests are moderately high, faintly striate and intermittently perforated ; their distal edges are in part smooth, in part finely denticulate. Crest nodes are strengthened by stout spines in some or all cases. The crests bordering the sulcus are very reduced.

REMARKS. Professor Georges Deflandre permitted the author and Mr. R. J. Davey to examine the holotype during visits to Paris, and also provided the photograph ; his courtesy is gratefully acknowledged.

Meiourogonyaux valensii sp. nov. is distinguished from the other species of this genus in the detail of tabulation and the nature of the crests.

OTHER SPECIES

The following species are here attributed to *Meiourogonyaux* gen. nov. and accord with the diagnosis of this genus :

Meiourogonyaux bulloidea (Cookson & Eisenack 1960b). Upper Jurassic (?Tithonian) ; Western Australia.

Meiourogonyaux cristulata (Sarjeant 1959). Middle Jurassic (Callovian) ; England.

A third species is doubtfully attributed to the genus :

?*Meiourogonyaux caytonensis* (Sarjeant 1959). Middle Jurassic (Callovian) ; England.

The mode of archaeopyle formation in this latter species is not clear. The holotype has an intact apex, but lacks plate 2", suggesting a precingular archaeopyle in a unique position : other specimens lack an apex. Assignment to *Meiourogonyaux* is thus provisional.

Genus *XIPHOPHORIDIUM* nov.

DERIVATION OF NAME. Greek, *xiphos*, sword : *phor-*, suffix meaning to bear, carry.

DIAGNOSIS. Proximo-chorate dinoflagellate cysts, spheroidal to ovoidal or polygonal with tabulation ?4', 1a, 6", 0-1p, 6'''', 1'''''. Cingulum strongly or weakly

spiral, laevo-rotatory. Apical and antapical horns lacking. Sutures marked by high crests bearing long, dagger-like spines, broadly spaced; crests bordering cingulum especially high and prominent. Surface smooth, granular, punctate or tuberculate. Archaeopyle formed by loss of apical plates; not all individuals have an archaeopyle.

TYPE SPECIES. *Hystrichodinium alatum* Cookson & Eisenack 1962b. Cretaceous (?Upper Aptian–Cenomanian); Western Australia.

REMARKS. This genus comprises forms with high, pronouncedly spinose crests. It is distinguishable from *Heliodinium*, *Hystrichodinium* and *Ctenidodinium* by the mode of archaeopyle formation, from *Heliodinium* and *Hystrichodinium* also by the fact that the sutural spines arise from crests; and from *Ctenidodinium* also by the fact that the cingulum is bordered on *both* sides by high crests.

***Xiphoridium alatum* (Cookson & Eisenack)**

Pl. 16, fig. 11

1962b. *Hystrichodinium alatum* Cookson & Eisenack: 478, pl. 2, figs. 1–4.

EMENDED DIAGNOSIS. A *Xiphophoridium* having an ovoidal to nearly globular shell, shell wall thin. Tabulation ?4', 1a, 6", 6"', ?Op, 1''' ; plates bounded by very high crests bearing long, dagger-like spines, crest curving inwards between bases of spines. Cingulum weakly spiral, of moderate breadth and bordered by especially high crests; sulcus also of moderate breadth, extending to antapex. Shell surface not, or only minutely, granular, bearing numerous tubercles, sometimes apparently arranged to plate margins, generally without obvious arrangement. Apical archaeopyle present.

HOLOTYPE. Specimen no. P.21272, National Museum, Victoria, Australia.

MATERIAL (figured). Geol. Surv. Colln. slide PF.3051(1). Chalk, H.M. Geological Survey Borehole, Fetcham Mill, Surrey, at 840 feet depth. Upper Cretaceous (basal Cenomanian).

DIMENSIONS. Holotype: overall length 125 μ , breadth 96 μ ; length of shell 70 μ , breadth 52 μ . Range of Australian specimens: overall lengths 100–102 μ , overall breadths 92–100 μ . As a result of orientation or preservation, it did not prove possible to obtain detailed measurements of the English specimens, but dimensions appear comparable.

DESCRIPTION. This species occurs infrequently throughout the English Cenomanian, some 20 specimens having been encountered. The specimen figured, seen in terminal view, was the best-preserved and allowed determination of the tabulation: all other specimens were damaged or distorted to some extent. It was not possible to prepare a satisfactory figure.

The shape of the archaeopyle is that of a ragged polygon with a narrow sulcal notch, suggesting that four apical plates were originally present. Six precingular plates are present, plate 6" being reduced to accommodate a quadrate anterior intercalary plate. Six postcingular plates are present ; no posterior intercalary plate could be distinguished in the specimens studied. The antapex is occupied by a single polygonal plate.

The cingulum is weakly spiral, laevorotatory ; its structure was not clear in the English specimens, but the photographs of the Australian specimens suggest a division into cingular plates (?6).

The crests are delicate, not or only minutely perforate : the spines arise simply as outgrowths of the crests and are somewhat flattened and dagger-like. The shell wall appears to lack ornament other than the tubercles.

REMARKS. In their original description of this species, Cookson & Eisenack noted the clear presence of tabulation and recognized this as a separating character from other species of *Hystriodinium*, in which they then placed it. They do not record the presence of an apical archaeopyle but this feature is suggested in one of their figures (pl. 2, fig. 2). The diagnosis is here emended to include reference to the tabulation and the possession of an apical archaeopyle.

Genus **BELODINIUM** Cookson & Eisenack 1960b : 249

TYPE SPECIES. *Belodinium dysculum* Cookson & Eisenack 1960b. Upper Jurassic (Tithonian) ; Australia.

REMARKS. This genus was diagnosed in the following terms :

" Shell elongate, unequally divided by a circular girdle. Main body marked into fields by delicate ledges : epitheca with a hollow membraneous horn, hypotheca with a flattened membraneous expansion."

In the absence of a full knowledge of the tabulation, distinction of this genus depends on the circular nature of the cingulum and the presence of an antapical pericoel. The description of the type species (Cookson & Eisenack 1960b : 250) makes it clear that archaeopyle formation is by loss of the apical plates. The authors state that their interpretation of the genus is " provisional " and " incomplete " : a fuller study of the genus and a revision of the diagnosis are clearly necessary before its status can be validly assessed.

Genus **MICRODINIUM** Cookson & Eisenack 1960a : 6

EMENDED DIAGNOSIS. Proximate dinoflagellate cysts, spheroidal to ovoidal in shape and usually small. Epitract smaller than hypotract. Tabulation 1', 0-?1a, 6", 6c, 6"', 1p, 1''', with differentiation in some species of additional plates in ventra, region. Cingulum broad, weakly spiral ; sulcus broad, extending from apex to antapex. Sutures bearing crests in form of low ridges (perforate or imperforate),

smooth, denticulate, or bearing spines of varying lengths ; alternatively sutures marked by lines of closely set spines. Shell surface smooth, granular, punctate or tuberculate. Archaeopyle formation by loss of single apical plate.

TYPE SPECIES. *Microdinium ornatum* Cookson & Eisenack 1960a. ?U. Aptian-Turonian : Australia.

REMARKS. At the time when it was proposed, this genus was technically invalid, since its tabulation falls within the limits specified for *Gonyaulax*. However, *Microdinium* is now recognized to be a cyst genus and, regarded as such, becomes a valid entity, since its tabulation does not accord with that of *Gonyaulacysta* either in the original definition of Deflandre or as here emended.

Representatives of this genus are relatively frequent in the English Cenomanian. The generic diagnosis is emended to accommodate variations in morphology exhibited by these forms.

Microdinium differs from the majority of fossil dinoflagellate cysts in having an apical archaeopyle ; from *Meiourogoniaulax* and *Xiphophoridium* in having only a single apical plate ; and from *Glyphanodinium* in having six precingular plates.

***Microdinium* cf. *ornatum* Cookson & Eisenack**

Pl. 16, figs. 3-6 ; Text-fig. 38

1960a. *Microdinium ornatum* Cookson & Eisenack : 6, pl. 2, figs. 3-8, text-figs. 2-4.

MATERIAL (Figured). Geol. Surv. Colln. slide PF.3050(1). Chalk, H.M. Geological Survey Borehole, Fetcham Mill, Surrey, at 670 feet depth. Upper Cretaceous (Upper Cenomanian).

DIMENSIONS. Figured specimen : length 40μ , breadth 32μ . Range length c.30-45 μ , breadth c.22-35 μ .

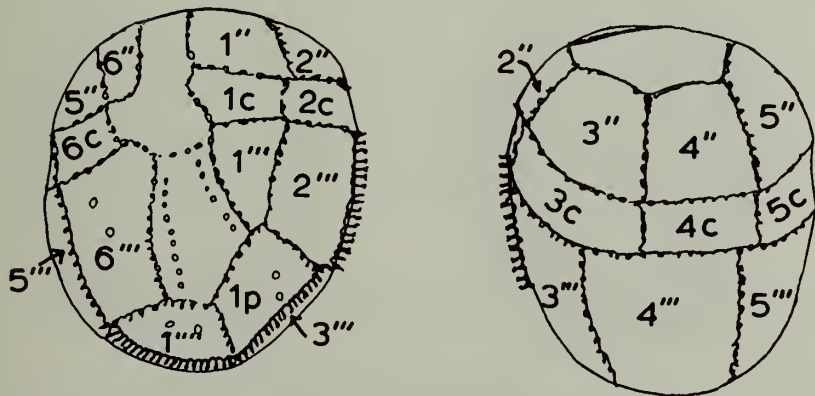


FIG. 38. *Microdinium* cf. *ornatum* Cookson & Eisenack. Tabulation. Left, ventral view ; right, dorsal view (the apex is missing). $\times$ c. 1250.

DESCRIPTION. This form occurred in moderate abundance in the upper levels of the Cenomanian of the Fetcham Mill Borehole, over 20 specimens having been seen ; the apex was missing in all specimens seen.

The shell is ovoidal in shape, with a somewhat flattened antapex and an apex truncated by the archaeopyle. Six precingular and six postcingular plates are present. The presence of an anterior intercalary plate was suggested in some specimens, but could not be confirmed as a result of distortion around the archaeopyle. Plates 1''' and 2''' are reduced to accommodate a large posterior intercalary plate ; this is of comparable size to the single antapical plate, some specimens indeed give the impression of having two antapical plates.

The cingulum is very broad and not hollowed ; it is weakly spiral, laevorotatory, its two ends scarcely differing in antero- posterior position. The sulcus is broad throughout its length, but broadest as it approaches the antapex : ventral plates are absent.

The shell surface is generally quite smooth, but bears a scatter of tubercles, some of which are aligned parallel to sutures ; the number and arrangement of tubercles varies between individuals. The sutures bear closely set spines, capitate and of constant length, giving almost the impression of perforate crests : in vertical view, these give the impression of a string of beads.

REMARKS. These English Cenomanian forms generally closely resemble *Microdinium ornatum* as described from Australia, but differ in two details—the absence of a plate separating the posterior end of the cingulum from the sulcus, and the form of the crests, which are constantly in the form of closely set spines. It is highly probable that they fall within the range of variation of *M. ornatum*, since they accord closely with the photographs and since Cookson & Eisenack state (p. 7) that “ the

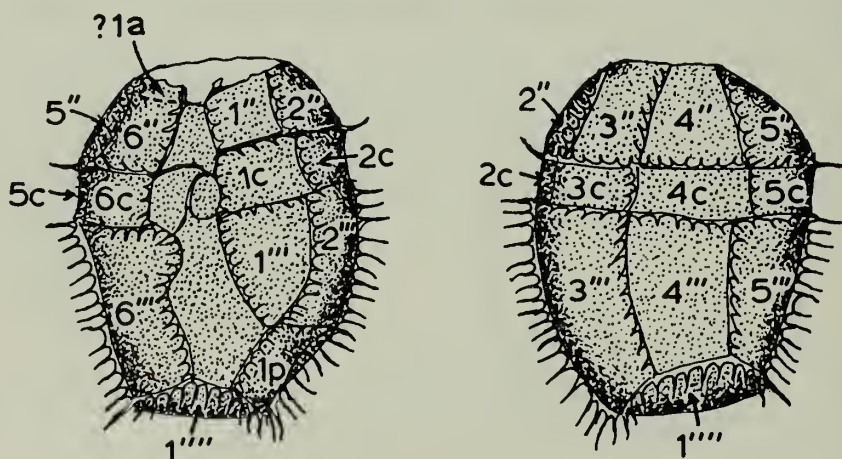


FIG. 39. *Microdinium setosum* sp. nov. Tabulation. Left, ventral view ; right, dorsal view. $\times$ c. 1250.

outer edge of the ledges may be missing " in some specimens ; it is also possible that representatives of two species have been placed together by those authors. For the present, it is considered appropriate that the English forms should be compared with, and not placed within, the species *M. ornatum*.

***Microdinium setosum* sp. nov.**

Pl. 16, figs. 9, 10 ; Text-fig. 39

DERIVATION OF NAME. Latin, *setosus*, bristly ; referring to the spines on the sutures.

DIAGNOSIS. A *Microdinium* having an ovoidal shell with somewhat flattened antapex. The epitract considerably smaller than the hypotract ; a broad cingulum, weakly spiral, divides them. Tabulation ?1', oa, 6", 6c, 6''', 1p, 1'''' : two additional plates present in ventral region between two ends of cingulum. Sutures bearing low crests from which arise spines of moderate length, simple and well spaced ; shell surface minutely but densely granular. Apex characteristically lost in the pylome formation.

HOLOTYPE. Geol. Surv. Colln. slide PF.3046(2). Chalk, H.M. Geological Survey Borehole, Fetcham Park, Surrey, at 840 feet depth. Upper Cretaceous (basal Cenomanian).

DIMENSIONS. Holotype : overall length 35μ , breadth 30μ ; shell length 33μ , breadth 24μ . Range of dimensions : overall lengths 33 to 38μ , breadths 24 to 37μ .

DESCRIPTION. This species is moderately abundant in the lower levels of the Cenomanian of the Fetcham Mill Borehole, over 30 specimens having been seen. The apex is presumed to have consisted of a single plate, but it was lost in the majority of specimens seen. In a few, the archaeopyle " lid " was still attached, but too buckled for its character to be determined.

Six precingular and six postcingular plates are present, the former being consistently smaller than the latter in the proportion that the epitract is smaller than the hypotract. Plates 1''' and 2''' are reduced : a posterior intercalary plate separates plate 2''' from the antapex. As in *M. cf. ornatum*, plate 1p and the antapical plate are of comparable size and in some specimens look more like paired antapical plates.

The cingulum is broad, not hollowed, and very weakly spiral, its two ends scarcely differing in antero-posterior position. It is divided into six cingular plates ; two ventral plates lie between its two ends and divide the sulcus into an epittractal and a hypottractal portion.

The crests are low and bear simple, flexuous spines, the crest margin being scalloped between spine bases. The surface bears a uniform, dense cover of minute granules.

REMARKS. *Microdinium setosum* sp. nov. differs from *M. ornatum* in crest character, detail of tabulation, and granular surface. It is placed in *Microdinium* on the basis of general structure and apical archaeopyle : possession of only one apical plate was presumed but not confirmed.

Genus **GLYPHANODINIUM** Drugg 1964

TYPE SPECIES. *Glyphanodinium facetum* Drugg 1964. Palaeocene (Danian) ; California, U.S.A.

REMARKS. This is a genus of distinctive proximate dinoflagellate cysts of pentagonal shape, with the tabulation ?1', oa, 6c, 6''', 1p, 1 p.v., 1''''', the archaeopyle being formed by loss of the single (?) apical plate. The cingulum is situated high on the test, the epitract being thus small, the hypotract large. The overall shell size is small. It differs from *Meiourogonyaulax* in the apparent number of apical plates, and from *Microdinium* in overall shape and the presence of only five precingular plates.

Genus **EISENACKIA** Deflandre & Cookson 1955 : 258

1954. *Eisenackia* Deflandre & Cookson : 1236 (name only).

EMENDED DIAGNOSIS. Proximate dinoflagellate cysts, spheroidal or ovoidal in shape, with the tabulation 2-3', 6'', ?6c, 6''', 2p, 1'''''; additional plates occupy ventral area, there being no sulcus as such. Plates consisting of raised areas of shell surface, isolated from one another by pattern of "channels" corresponding in position to sutures. (It is here proposed that such inverse equivalents of sutures be termed "fossae".) Cingulum weakly helicoid. Shell surface typically reticulate, possibly also granular or punctate. Apical archaeopyle formed by loss of apical plates.

TYPE SPECIES. *Eisenackia crassitabulata* Deflandre & Cookson 1955. Paleocene to Lower Eocene ; Australia.

REMARKS. The diagnosis is emended to stress the characteristic form of the tabulation, as plates separated by fossae, and to include reference to the mode of archaeopyle formation. The latter character was remarked on by Deflandre & Cookson (1955 : 260) in the description of the type species.

C. Genera with epitracial archaeopyle

Genus **RHAETOGONYAULAX** nov.

DERIVATION OF NAME. Refers to the occurrence of the type species in the Rhaetian (Rhaetic) Stage, uppermost Triassic, and to possession of a *Gonyaulax* type of tabulation.

DIAGNOSIS. Proximate dinoflagellate cysts, spindle-shaped or biconical, typically with the tabulation 4', 1a, 6'', 6''', 1p, 1''''': tabulation well or poorly marked by ridges or partially or entirely indeterminate. Cingulum strongly or weakly spiral, laevorotatory, divided into plates (?6c) or without such division. Surface smooth, granular, nodose, punctate or reticulate ; ornamentation may mask the tabulation. Archaeopyle (where present) epitracial, formed by schism of shell immediately anterior to cingulum.

TYPE SPECIES. *Gonyaulax rhaetica* Sarjeant, 1963a. Upper Triassic (Rhaetic) ; England.

REMARKS. This genus is created to accommodate the earliest known species having a tabulation of *Gonyaulax* type. The shape is unlike that of any other known fossil species having such a tabulation ; the plate boundaries are so poorly marked as to make it seem probable that any descendants would be non-tabulate. For these reasons, it is considered that a relationship with the species attributed to the genus *Dichadogonyaulax* gen. nov. is unlikely. Later genera having a spindle-shaped outline (*Kalypte* ; *Netrellytron*) appear to consistently form precingular archaeopyles.

OTHER SPECIES

The following species also accords with the diagnosis of this genus and is here included in *Rhaetogonyaulax* accordingly : *Rhaetogonyaulax chaloneri* (Sarjeant 1963a). Upper Triassic (Rhaetic) ; England.

Genus *DICHADOGONYAULAX* nov.

DERIVATION OF NAME. Greek, *dichados*, half : refers to the almost median schism of the shell, so that typically half shells are encountered, and to the *Gonyaulax*—type tabulation.

DIAGNOSIS. Proximate dinoflagellate cysts, spheroidal, ovoidal, ellipsoidal or polyhedral, having the tabulation 3-5', 0-?1a, 6'', 5 6''', 1p, 1'''' : sulcus divided into plates or undivided, ventral region may show division into additional small plates. Cingulum strongly or weakly spiral, laevorotatory. Apical horn may be present ; median and antapical horns lacking. Sutures in form of low ridges bearing crests of varied form (smooth, denticulate or spinous ; perforate or imperforate) ; or marked by lines of spines. Archaeopyle (where present) epittractal, by schism of shell immediately anterior to cingulum.

TYPE SPECIES. *Gonyaulax culmula* Norris 1965. Upper Jurassic (Portlandian) ; England.

REMARKS. Norris (1965) has described a group of species from the Portlandian which have in common their general morphology and mode of archaeopyle formation, but whose tabulation accords sometimes to the *Gonyaulax* pattern, sometimes to that of *Leptodinium*. The tabulation of the type species, which lacks an anterior intercalary plate but possesses six postcingular plates, is indeed intermediate in character. On this basis, it is considered that common characters outweigh the small tabulation differences and that the diagnosis should embrace all forms with epittractal archaeopyles and generally similar morphology.

OTHER SPECIES

The following species also accord with the diagnosis of this genus :

Dichadogonyaulax pannea (Norris 1965) comb. nov. Upper Jurassic (Upper Kimmeridgian-Portlandian) ; England.

D. schizoblata (Norris 1965) comb. nov. Upper Jurassic (Upper Portlandian) ; England.

D. Genera with cingular archaeopyle

Genus *CTENIDODINIUM* Deflandre 1938 : 181

EMENDED DIAGNOSIS. Proximo-chorate dinoflagellate cysts, spheroidal, ovoidal, ellipsoidal or polygonal, having the tabulation 3-4', 0-1a, 6'', 6c, 6''', 1p, 0-1 p.v., 1''''; sutures in form of low ridges bearing crests of varied form, typically but not constantly high and denticulate. Cingulum strongly or weakly spiral, laevo-rotatory; suture on anterior margin of cingulum lacking crest, crest on posterior margin very high. Archaeopyle (where present) formed by schism along cingulum.

TYPE SPECIES. *Lithodinia jurassica* var. *ornata* Eisenack 1935. Middle Jurassic (Callovian); Germany.

REMARKS. The diagnosis is emended to include reference to tabulation and mode of archaeopyle formation; the latter, in combination with the unequal crest development on either side of the cingulum, characterizes the genus. Both species currently attributable to the genus occur in the Middle to Upper Jurassic (Callovian to Oxfordian), the type species being known to range up into the Lower Oxfordian.

OTHER SPECIES

The following species also accords with the revised diagnosis of the genus :

Ctenidodinium tenellum Deflandre 1938. Upper Jurassic (Oxfordian); France.

Genus *WANAEA* Cookson & Eisenack 1958 : 57

TYPE SPECIES. *Wanaea spectabilis* Cookson & Eisenack 1958. Upper Jurassic; New Guinea.

REMARKS. W. R. Evitt, in litt., has informed the writer that this genus comprises detached epitraits and hypotraits of a genus with a *Gonyaulax*-pattern tabulation. High crests, perforated in varying degree to give a fringe-like appearance, border the cingulum: crests elsewhere on the shell are marked only by low ridges. Archaeopyle formation apparently results from schism along the cingulum, but the mechanism of the process appears more complicated than in *Ctenidodinium*. A full study of the genus is understood to be in press.

E. Genera with archaeopyles formed by other means

Genus *PLURIARVALIUM* Sarjeant 1962a : 260

TYPE SPECIES. *Pluriarvalium osmingtonense* Sarjeant 1962a. Upper Jurassic (Upper Oxfordian); England.

Pluriarvalium osmingtonense Sarjeant

Text-fig. 40

1962a. *Pluriarvalium osmingtonense* Sarjeant : 262, pl. 1, fig. 5; text-fig. 6.

REMARKS. This species is relatively abundant in certain horizons of the Upper Jurassic; all specimens observed to date are either intact or severely damaged and

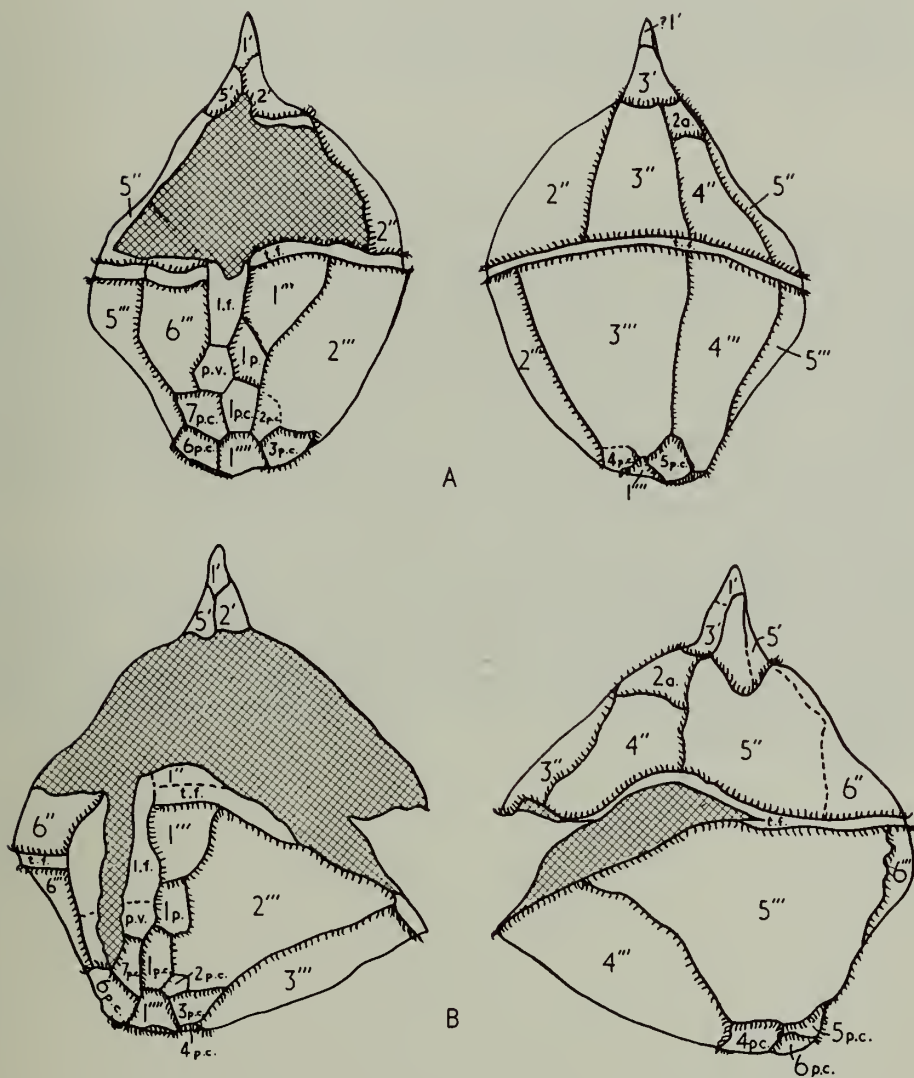


FIG. 40. *Plurivarvalium osmingtonense* Sarjeant. Two damaged specimens, showing how the anterior portion of the ventral surface is apparently lost in archaeopyle formation. Left, ventral view; right, dorsal view. $\times$ c. 500.

crumpled. Study of the damaged specimens suggests that archaeopyle formation may occur by loss of the anterior ventral surface (see Text-fig. 40) : such a method has not been observed in any other known dinoflagellate cyst. Further studies are needed before this suggestion can be confirmed ; but certainly, no specimens yet observed give suggestion of archaeopyle formation by more familiar methods.

The holotype and paratypes of this species are in the collections of the Micro-palaeontology Laboratory, Department of Geology, University of Sheffield.

CONCLUSIONS

The characteristics and known stratigraphic distribution of the twenty-one valid genera here considered are summarized in the accompanying Table. At present, no coherent picture emerges regarding the stratigraphical distribution of the different archaeopyle types : fuller studies of critical intermediate assemblages are clearly necessary. All four principal modes of archaeopyle formation were operative by the Upper Jurassic and it seems likely that these represent four divergent lines of evolution. *Rhaetogonyaulax* may represent a trend towards non-tabulate cysts of spindle-shape ; *Acanthogonyaulax* towards non-tabulate, densely spinose forms ; and the ancestors of *Hystrichosphaera* may well be found in species of *Gonyaulacysta* with progressively lower crests bearing progressively higher spines.

Dinoflagellate cysts basically having a *Gonyaulax*-type tabulation are shown to be dominant elements in Upper Jurassic and Lower Cretaceous assemblages, declining in importance (*Hystrichosphaera* excepted) in the Upper Cretaceous ; rare in the lowest Tertiary ; and apparently not represented after the Eocene. Their stratigraphic importance is thus greatest in the Upper Jurassic and Lower Cretaceous, where rapid evolution and limited vertical range combine to render many species satisfactory zonal indices.

TABLE 4

GENUS	TABULATION								FORM OF SUTURES	TYPE OF ARCHAEOPOYLE	OTHER SPECIAL FEATURES	OVERALL SHELL FORM	KNOWN STRATIGRAPHIC RANGE
	Apical plates	Intercalary	Precingular Plates	Cingular Plates	Postingular Plates	Posterior Intercalary Plates	Antapical Plates	Additional Plates (If present)					
<u>Rhoetogonyaulox</u>	4	1	6	6	6	1	1	—	LOW RIDGES OR INDETERMINABLE	EPITRACTAL	SPINDLE SHAPED SHELL	PROXIMATE	U. Triassic (Rhoetion)
<u>Gonyaulocysto</u>	3-4	0-1	6	6	6	1	1	0-1 p.v. Ventral plates sometimes present	CRESTS OR LINES OF SPINES (HEIGHT LESS THAN 1/4 SHELL DIAMETER)	PRECINGULAR	APICAL HORN OFTEN PRESENT	PROXIMATE	M. Jurassic (Bojocion) to U. Cretaceous (Senonian)
<u>Meiourogonyaulox</u>	4	0-1	6	6	5-6	0-1	—	0-1 p.v.	LOW RIDGES OR CRESTS	APICAL	—	PROXIMATE	M.-U. Jurassic (Bothonian - ?Tithonian)
<u>Ctenidodinium</u>	3-4	0-1	6	6	6	1	1	0-1 p.v.	CRESTS	CINGULAR	HIGH CREST POSTERIOR TO CINGULUM: NO CREST ON ANTERIOR SIDE	PROXIMO-CHORATE	M.-U. Jurassic (Collovion - Oxfordion)
<u>Acanthogonyaulox</u>	3-4	0-1	6	6	6	1	1	—	LINES OF SPINES	PRECINGULAR	GENERAL SPINE COVER	PROXIMATE	U. Jurassic (Oxfordion - Kimmeridgion)
<u>Wonoea</u>	—	Not determined in detail							LOW RIDGES EXCEPT ALONGSIDE CINGULUM	CINGULAR	HIGH, FRINGE LIKE CRESTS BORDERING CINGULUM	PROXIMO-CHORATE	U. Jurassic (Oxfordion - Tithonian)
<u>Pluriarvolium</u>	?5	2	6	?6	6	1	1	1 p.v., up to 7 posterior circle plates	LOW RIDGES	? BY LOSS OF ANTERIOR VENTRAL SURFACE	—	PROXIMATE	U. Jurassic (U. Oxfordion)
<u>Leptodinium</u>	4	0	6	5-6	5	1	1	—	CRESTS OR LINES OF SPINES (HEIGHT LESS THAN 1/4 SHELL DIAMETER)	PRECINGULAR	—	PROXIMATE	U. Jurassic (Oxfordion) - Oligocene
<u>Belodinium</u>	—	Not determined in detail							DELICATE CRESTS	APICAL	APICAL HORN ANTAPICAL PERICOEL	PROXIMATE	U. Jurassic (Tithonian)
<u>Oichodogonyaulox</u>	3-5	0-?1	6	6	5-6	1	1	Ventral plates sometimes present	CRESTS OR LINES OF SPINES	EPITRACTAL	—	PROXIMATE	U. Jurassic (Portlandion)
<u>Heslertonio</u>	3-4	0-1	6	6	6	1	1	0-1 p.v.	VERY HIGH CRESTS (GREATER THAN 1/4 SHELL DIAMETER)	PRECINGULAR	—	CHORATE	L.-U. Cretaceous (Hauterivion - Cenomanion)
<u>Heliodinium</u>	?3	?0	6	?0	6	?0	1	—	DAGGER LIKE SPINES ARISING FROM LOW CRESTS	PRECINGULAR	SUTURAL SPINES FLAT, FLEXIBLE	PROXIMO-CHORATE	L.-U. Cretaceous (Hauterivion - Cenomanion)
<u>Hystrichodinium</u>	—	Not determined in detail							LONG SPINES ARISING FROM POSITIONS OF SUTURES	PRECINGULAR	SUTURAL SPINES ROUNDED, STIFF	PROXIMO-CHORATE	L.-U. Cretaceous (Hauterivion - Senonian)
<u>Corpodinium</u>	?	?6	6	?	6	?	?	—	CRESTS	PRECINGULAR	—	PROXIMATE	U. Cretaceous (Aptian - Albion)
<u>Microdinium</u>	1	0-?1	6	6	6	1	1	Ventral plates sometimes present	LOW CRESTS OR LINES OF SPINES	APICAL	EPITRACT SMALLER THAN HYPOTRACT	PROXIMATE	L.-U. Cretaceous (?U. Aptian - Turonian)
<u>Xiphophoridium</u>	?4	1	6	?6	6	0-1	1	—	VERY HIGH CRESTS ESPECIALLY BORDERING CINGULUM	APICAL	—	PROXIMO-CHORATE	L.-U. Cretaceous (?U. Aptian - Cenomanion)
<u>Psalignonyaulox</u>	3-4	1	6	6	6	1	1	—	CRESTS	PRECINGULAR	APICAL AND ANTAPICAL PERICOELS	BICAVATE	U. Cretaceous (Cenomanion) - Tertiary
<u>Hystrichosphoeropsis</u>	?3-4	?1	6	6	6	1	1	—	CRESTS WITH SPINES AT NODES	PRECINGULAR	APICAL AND ANTAPICAL PERICOELS	BICAVATE	U. Cretaceous (Tertiary)
<u>Rophidodinium</u>	—	Not determined in detail							LOW, BEARING FEW VERY LONG SPINES	NOT REPORTED	SPINES STIFF UP TO TWICE SHELL LENGTH	CHORATE	U. Cretaceous
<u>Glyphonodinium</u>	?1	0	5	6	6	1	1	1 p.v.	LOW CRESTS	APICAL	EPITRACT SMALLER THAN HYPOTRACT	PROXIMATE	Paleocene
<u>Eisenackia</u>	2-3	0	6	?6	6	2	1	Ventral plates sometimes present	FOSSAE	APICAL	—	PROXIMATE	Paleocene - L. Eocene

Characteristics and stratigraphical distribution of fossil Dinoflagellate cyst genera having a tabulation according with the *Gonyaulax* pattern.

VII. FOSSIL DINOFLAGELLATE CYSTS ATTRIBUTED TO *BALTISPHAERIDIUM*

By R. J. DAVEY, C. DOWNIE,

W. A. S. SARJEANT & G. L. WILLIAMS

INTRODUCTION

The genus *Baltisphaeridium* was proposed by Eisenack (1958 : 398) to accommodate species of fossil microplankton having spherical to oval, nontabulate shells bearing simple or branching appendages, consistently closed distally. The type species selected was the Silurian species *B. longispinosum*, having a size range of 40 to 75 μ . Eisenack did not compare his new genus with the existing genus *Micrhystridium* Deflandre 1937 (defined as having a shell diameter inferior to 20 μ) : subsequent workers, however, assumed a separation between the two genera on the basis of the size restriction of *Micrhystridium*.

Staplin (1961 : 408) proposed the redefinition of *Micrhystridium* by restricting it to forms having appendages closed distally and by removing the size restriction ; this redefinition made *Baltisphaeridium* into a junior synonym of *Micrhystridium*. This proposal was attacked by Eisenack (1962 : 96) and Downie & Sarjeant (1963 : 83-84) ; the latter authors, while recognizing the arbitrary nature of the upper size limit of *Micrhystridium*, nevertheless considered that this genus expressed a natural morphological grouping distinct from *Baltisphaeridium*. They proceeded to give an emended diagnosis for *Baltisphaeridium*, as follows :

“ Hystrichospheres with spherical to oval shells not divided into fields or plates, bearing $\pm$ numerous processes, simple, branching or ramifying, hollow to solid, always with closed tips. The processes are not connected together distally and no outer shell, complete or incomplete, is present : the processes are most often of a single basic type, but processes of two or more types may be present. Mean and modal diameter of the shell greater than 20 μ . ”

At this date, separation of acritarchs from dinoflagellate cysts had not been made. Within the genus *Baltisphaeridium*, there were placed forms having pylomes ; forms with archaeopyles, variously situated ; and forms having no openings of any kind. Thus, within a single genus, there were classed together both species of demonstrable dinoflagellate affinity and morphologically similar forms of unproven and perhaps quite different affinity.

An attempt is here made to remedy this confused situation. Species having spheroidal to ovoidal shells with apical archaeopyles, with the processes arranged so as to give a reflected tabulation 4', 0a, 6'', 6c, 6''', 1p, 3''''', are placed into the new genus *Surculosphaeridium*. Species having a spheroidal to ovoidal shell with an apical archaeopyle, but having numerous processes and an undetermined or intermediate tabulation, are placed in a second new genus, *Cleistosphaeridium*. Species having an elongate ovoidal to ellipsoidal shell, with an apical archaeopyle and processes arranged into distinct rows, are placed in a third new genus *Prolixosphaeridium*. Species having a precingular archaeopyle are placed in a fourth new genus *Exochosphaeridium*. The residue of species, either with a circular pylome (such as the type species, *B. longispinosum*) or with no observed opening, are considered to be acritarchs and left

within the genus *Baltisphaeridium*. A full restudy of this latter genus has recently been published by Staplin, Jansonius & Pocock (1965) ; a consideration of their revisions and proposals is outside the scope of the present paper.

The Species *hirsutum* (Ehrenberg) and *striolatum* (Deflandre).

Ehrenberg (1838) recorded the occurrence, in Cretaceous flints from Delitzsch, Saxony, of microplankton having simple, oval shells bearing a scatter of simple spines of moderate length. These he named "*Xanthidium hirsutum*(?)", thus implying their identity with a modern Desmid, now designated *Staurostrum hirsutum* (Ehr.) Ralfs 1848.

Reade (1839) illustrated under this name two quite distinct Upper Cretaceous forms, one having a scatter of long, stout, simple spines, the other a dense mat of very short, fine spines ; neither resembles Ehrenberg's figures at all closely. The second of Reade's forms was also figured, again as *X. hirsutum*, by White (1842) and has subsequently been designated a distinct species, *Baltisphaeridium whitei* (Deflandre & Courteville 1939) Downie & Sarjeant 1963.

Pritchard (1841 : 187, pl. 12, fig. 512) figured as *X. hirsutum* a fourth morphologically distinct form from the Upper Cretaceous globular, and with a very sparse cover of short, stout spines. This clearly represents a distinct species, but it has not been redescribed and the holotype is lost.

In 1932, O. Wetzel illustrated a form from the Baltic Upper Cretaceous, which he named *Hystrichosphaera hirsuta* forma *minor* (pl. 3, fig. 13) ; this was described and refigured by him (1933 : 91, pl. 4, fig. 26). It was of small size (shell diameter 24–28 μ) with numerous (50–60) simple, stout spines of moderate length, quite comparable to Ehrenberg's figure. Forms from the Dutch Upper Cretaceous were described and figured as forma *minor* by de Wit (1943 : 381–83) ; his text-figure 9a corresponds broadly to Wetzel's description, but his text-figure 9b shows a form with very numerous, extremely abbreviate spines, quite unlike Wetzel's description and constituting yet a sixth morphological type!

Wetzel also described and figured a second form, which he named *H. cf. hirsuta* forma *varians* (1932, pl. 3, fig. 11 ; 1933 : 93, pl. 4, figs. 27–29). This has quite long spines, sometimes branching at their tips, and a shell surface bearing a pattern of low ridges. One of his figures (pl. 4, fig. 29) indicates possession of an archaeopyle. Forms from the Dutch Upper Cretaceous were figured under this name by de Wit (1943, text-fig. 10a, b).

In 1937, Deflandre transferred the species *hirsutum* to his genus *Hystrichosphaeridium*, commenting : " It is quite certain that neither of the forms described by O. Wetzel . . . corresponds to the species of Ehrenberg." He suggested, but did not firmly propose, elevation of forma *minor* to specific status, as *Hystrichosphaeridium minor*. In the same paper, a new Upper Cretaceous species was described, having a surface divided into more or less triangular, concave fields and bearing appendages of very variable character (relatively slender, simple or branching spines, together

with broader processes, branching strongly and with tips secondarily branched), the bases of adjacent appendages being connected by striae on the shell surface. This was named *Hystrichosphaeridium striolatum* (Deflandre 1957 : 72, pl. 15, figs. 1, 2); it was again figured by Deflandre & Courteville (1939, pl. 3, fig. 2).

In 1941, Maria Lejeune-Carpentier re-examined Ehrenberg's material and relocated the holotype ; it is contained in Slide XXVI of his series " Feuerstein von Delitzsch " and is in the Institut für Paläontologie und Museum der Humboldt-Universität, Berlin ; it is labelled in pencil " *X. hirtum* ", obviously in error. Lejeune-Carpentier comments wryly : " C. G. Ehrenberg published . . . only a very rough drawing, as likely to mislead his successors as to guide them." Her re-examination showed the shell surface to be divided into striated fields ; the appendages were normally simple and several were found to be " united in pairs by a sort of web." She concluded : " What seems certain is the identity of *H. striolatum* Defl. with Ehrenberg's species " and she retained the name *hirsutum* for this conjoint species.

De Wit (1944) figured a form from the Dutch Upper Cretaceous as *H. hirsutum* (unnumbered text-figure). This had simple, stiff spines : it closely resembled one of the forms he had previously figured (1943, text-fig. 10a) as *H. hirsutum* forma *varians* and also resembled Ehrenberg's figures, but the species represented does not accord with Lejeune-Carpentier's redescription of the holotype.

In 1946, Deflandre discussed the taxonomic position and commented : " The figure of Ehrenberg . . . has as legend " *X. hirsutum* (?) from a flint from Delitzsch," *X. hirsutum* (without ?) being given as ' living at Berlin ' . . . It is thus not possible now to utilize the name *X. hirsutum* Ehr. and to make of it a *Hystrichosphaeridium hirsutum* (Ehr.), as Maria Lejeune-Carpentier wishes and . . . with very diverse meanings. The microfossil rediscovered at Berlin, whether or not it served as a model for Ehrenberg, being, according to Mme. Lejeune-Carpentier, identical to *H. striolatum* Defl., must thus be catalogued under this latter name."

Deflandre's comments and proposals are wholly correct. However, in 1948, André Pastiels described Eocene forms from Belgium under the names *Hystrichosphaeridium* cf. *hirsutum* Ehrbg. and *H.* cf. *hirsutum* forma *minor*. Subsequently Cookson (1953) described an Australian Tertiary form as *H.* cf. *hirsutum* : and Cookson & Eisenack (1958) applied this name to globular forms with short, simple spines from the Lower Cretaceous of Australia and Papua. In 1960, Klement, mentioning this form in discussion, transferred it to the genus *Baltisphaeridium*. A further complication was introduced by W. Wetzel (1952 : 401). On the basis that Ehrenberg's type specimen, when re-located by Lejeune-Carpentier, bore the manuscript name *H. hirtum* (interpreted by her as an accidental mis-spelling), he employed the name *Hystrichosphaeridium hirtum* for forms from the Baltic Danian. He figured three forms as " *H.* cf. *hirtum* " (1952, text-figs. 17-19). One of these is spherical, with moderately long, simple spines (text-fig. 17) ; the second (text-fig. 18) is oval in outline, with simple spines of moderate length ; and the third (text-fig. 19) is also ovoidal, with long, simple or branching spines. The two latter forms are in fact more comparable to *Prolixosphaeridium xanthiopyxides* (Deflandre). Wetzel

further complicated matters by designating other forms "*H. cf. striolatum*" (pp. 399-400, text-figs. 13, 14) : both forms show "archaeopyles", but neither appears truly comparable to Deflandre's species.

In a second paper describing Danian assemblages, Wetzel (1955 : 38, text-fig. 11) reiterated his proposals and described a new form, under the name *H. hirtum* subsp. *amplum*. The text-figure shows a spherical form with short, stiff spines, again more approaching Ehrenberg's text-figure than the specimen as redescribed.

The name *striolatum* has been employed in equal measure—by Valensi (1955 : 593, pls. 4, fig. 10 ; pl. 5, fig. 3) in describing French Cretaceous forms from Magdalenian worked flints ; by Gocht (1959 : 73, pl. 7, fig. 10) who described forms from the German Lower Cretaceous as *H. cf. striolatum* ; and by Górka (1963 : 68-70, pl. 10, fig. 6-7, text-pl. 8, figs. 5-6) who used the same name to designate forms from the Upper Cretaceous of Poland.

Downie & Sarjeant (1963, pp. 91-2) compromised by including both names (*hirsutum* and *striolatum*) in their list of species attributable to *Baltisphaeridium*. Similarly, both names figure in their list of valid taxa (Downie & Sarjeant 1964: 91, 97). In the latter work, *hirtum* is listed as an invalid alteration of *hirsutum* (p. 166).

The present situation thus remains confused. One of the authors (R.J.D.) was permitted, through the courtesy of Prof. Deflandre, to make a full re-examination of the holotype of *striolatum* which confirmed that Ehrenberg's and Deflandre's species are conspecific. For the reasons enunciated by Deflandre (1946), the species must be designated *striolatum*. The name *hirtum*, whether or not originally written in error, was merely pencilled on to a slide by Ehrenberg and was not validly published until 1952. It is therefore either an invalid alteration of the name *hirsutum* or a junior synonym of *striolatum* ; however regarded, it cannot be retained.

The holotype of the species *striolatum* (in the laboratoire de Micropléontologie, École Pratique des Hautes Études, Paris, preparation AH 89, flint S.52) is contained in a flint flake. It is here provisionally included in the new genus *Exochosphaeridium*, on the basis of similarity in general structure to the type species, *E. phragmites*. However, the apical process characteristic of the genus was not certainly observed, nor was an archaeopyle noted.

In view of the highly doubtful character of the morphology of the three subspecies *amplum* W. Wetzel, *minor* O. Wetzel and *varians* O. Wetzel, it is considered that their erection to specific status would be inappropriate until a full restudy of the holotypes has been undertaken. They are therefore provisionally regarded as subspecies of *E. striolatum*.

Genus *SURCULOSPHAERIDIUM* nov.

DERIVATION OF NAME. Latin, *surculus*, branch or twig ; *sphaera*, a ball—with reference to the branched nature of the processes radiating from the central body.

DIAGNOSIS. Subspherical chorate cysts bearing a moderate number of intratabular processes, considered to reflect the tabulation 4', 6'', 6c, 6''', 1p, 3'''''. Processes solid, closed distally and branched. Archaeopyle apical.

TYPE SPECIES. *Hystrichosphaeridium cribrotubiferum* Sarjeant 1960. Upper Jurassic (*Cardioceras cordatum* Zone) ; England.

REMARKS. The processes usually show a distinct circular arrangement on the surface of central body. The cingular processes are distinctive, being deeply furcate, and with the archaeopyle make orientation easy.

***Surculosphaeridium cribrotubiferum* (Sarjeant)**

Pl. 9, fig. 6 ; Text-fig. 41

1960. *Hystrichosphaeridium cribrotubiferum* Sarjeant : 137, pl. 6, figs. 2, 3, text-fig. 1.

EMENDED DIAGNOSIS. Subspherical central body bearing moderate number of solid, distally closed, perforate processes. Processes variably branched, sometimes deeply, especially cingular processes. Processes reflect a tabulation of 4', 6'', 6c, 6''', 1p, 3'''''.

HOLOTYPE. B.M.(N.H.) slide V.51735(1). Upper Jurassic (Oxford Clay, *Cardioceras cordatum* Zone) ; England.

DIMENSIONS. Holotype : overall diameter 75 μ , diameter of central body 43 by 39 μ , length of processes up to 24 μ . Range : overall diameters 60–80 μ . Number of specimens measured, 8.

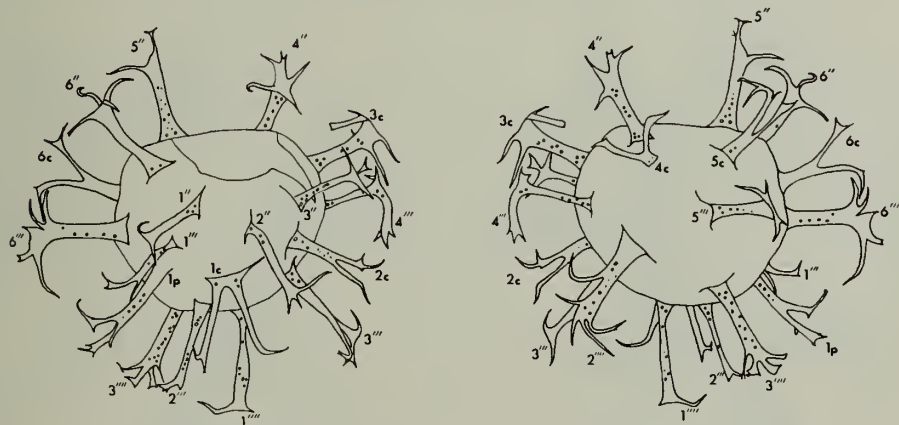


FIG. 41. *Surculosphaeridium cribrotubiferum* (Sarjeant). Holotype. Tabulation as reflected by the processes. Left, oblique ventral view ; right, oblique dorsal view. $\times$ c. 600.

REMARKS. The diagnosis of this species has been emended to draw attention to the closed processes, which reflect a definite tabulation characteristic of the genus and the presence of an archaeopyle. The processes were originally considered to be open distally ; however, full re-examination of the holotype at high magnifications has not confirmed this.

***Surculosphaeridium vestitum* (Deflandre)**

Pl. 9, fig. 8 ; Text-fig. 42

1938. *Hystrichosphaeridium vestitum* Deflandre : 189, pl. 11, figs. 4-6.
 1938. *Hystrichosphaeridium vestitum* Deflandre ; Deflandre : 688, text-fig. 3.
 1947. *Hystrichosphaeridium vestitum* Deflandre ; Deflandre, text-fig. 1, no. 3.
 1952. *Hystrichosphaeridium vestitum* Deflandre ; Deflandre, text-fig. 7.
 1955. *Hystrichosphaeridium vestitum* Deflandre ; Valensi : 587, pl. 2, fig. 8.
 1960c. *Baltisphaeridium vestitum* (Deflandre) Sarjeant : 397, pl. 13, fig. 8, pl. 14, figs. 13, 14.
 1962a. *Baltisphaeridium vestitum* (Deflandre) : Sarjeant, pl. 12, figs. 3, 5, 6.

REMARKS. The holotype, from the Oxfordian of France, has been restudied by two of the authors (R.J.D. and W.A.S.S.), through the courtesy of Prof. Deflandre ; and the specimens figured by Sarjeant (1962a) from the Oxfordian of England have also been re-examined in the light of recent studies. The processes of this species are extremely variable in form, so making the elucidation of the reflected tabulation very difficult. The processes are intratabular, the larger ones reflecting one plate of the original dinoflagellate theca, while some of the finer ones, in contrast, occur in twos and threes and represent a larger process which has been subdivided down to the surface of the central body. Thus two or three of these processes may reflect a single plate. The most distinctive and characteristic processes are the ones lying in the cingular zone. These are either deeply furcate or completely divided into two finer



FIG. 42. *Surculosphaeridium vestitum* (Deflandre). Position of cingular processes. Left, dorsal view ; right, ventral surface by transparency. V.51736(1). $\times$ c. 650.

processes. Such cingular processes are especially characteristic of the genus *Surculosphaeridium*, and make specimen orientation comparatively easy. The form of the processes and the exact distribution of the non-cingular processes, although difficult to determine, indicate that this species does belong to this genus.

MATERIAL (figured). B.M.(N.H.) slide V.51736(1). Lower Oxfordian, Dorset, England. Upper Jurassic, England.

DIMENSIONS. Figured specimen : diameter of central body 37 by 47 μ , length of processes up to 30 μ .

Surculosphaeridium longifurcatum (Firtion)

Pl. 8, figs. 7, 11, Text-figs. 43, 44

1952. *Hystrichosphaeridium longifurcatum* Firtion : 157, pl. 9, fig. 1 ; text-fig. 1, H, K, L and M.

1963. *Baltisphaeridium longifurcatum* (Firtion) Downie & Sarjeant : 91,

DESCRIPTION. A number of specimens have been found in the British Cenomanian which appear to be comparable to Firtion's species from the Cenomanian of France.

The central body is subspherical. The periphragm is smooth and gives rise to a more or less constant 26 processes in a complete specimen. An angular archaeopyle is commonly present, the detached apical region bearing 4 apical processes. The processes are closed distally and are rather variable in form, being simple, lobate foliate or digitate. Some of the processes, particularly those marking the cingulum, are deeply branched. In the Upper Cenomanian particularly, the cingular processes, each reflecting a cingular plate, may be completely subdivided. Thus there appears to be two instead of one cingular process for each plate.

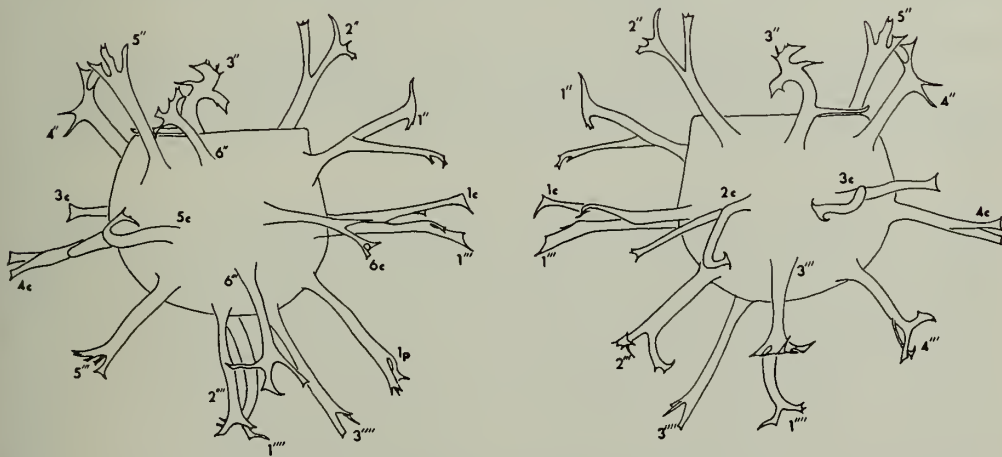


FIG. 43. *Surculosphaeridium longifurcatum* (Firtion). Tabulation as reflected by the processes. Left, top lateral view ; right, bottom lateral view. PF.3042(1). $\times$ c. 800.

The presence of an apical archaeopyle and the distinctive deeply furcate cingular processes make orientation of this species relatively easy. A number of well preserved specimens were studied and from the positions of the intratabular processes the reflected tabulation appeared to be 4', 6'', 6c, 6''', 1p, 3'''. The test of the original dinoflagellate is tentatively reconstructed in the accompanying figure (Text-fig. 41).

The reflected tabulation of *S. longifurcatum* is the same as in *S. cribrotubiferum* (Sarjeant, 1960) ; however, the latter possesses characteristically perforate processes.

MATERIAL (Figured). Pl. 8, fig. 11, Geol. Surv. Colln. PF.3042(1). Lower Chalk, H.M. Geological Survey Borehole, Fetcham Mill, Surrey at 840 feet depth. Upper Cretaceous (Cenomanian). Another specimen, Pl. 8, fig. 7, FM.730/2, at 730 feet depth.

DIMENSIONS. Figured specimens : diameter of central body 32 by 37 μ , length processes 20–24 μ . Range, lateral view : diameter of central body 30–47 μ ; apical view : diameter of central body 36–50 μ ; length of processes 14–29 μ . Mean diameter of archaeopyle, 20 μ . Number of specimens measured, 24.

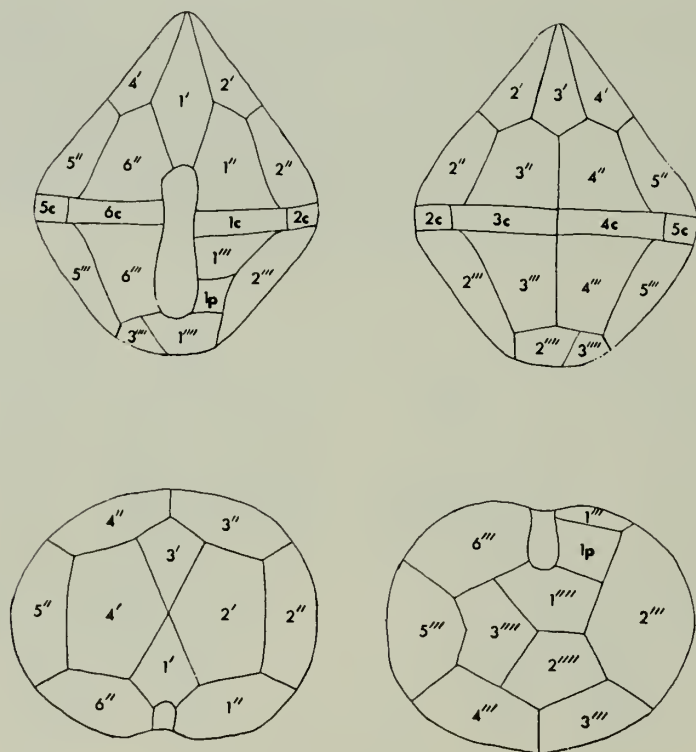


FIG. 44. *Surculosphaeridium longifurcatum* (Firtion). The probable original tabulation of the dinoflagellate.

Genus *EXOCHOSPHAERIDIUM* nov.

DERIVATION OF NAME. Greek, *exochos*, projecting or prominent ; *sphaera*, ball—with reference to the distinctive nature of the apical process.

DIAGNOSIS. Subspherical chorate cysts bearing numerous, commonly simple, closed processes. Apical process larger than normal processes and irregularly branched. Archaeopyle precingular.

TYPE SPECIES. *Exochosphaeridium phragmites* sp. nov. Upper Cretaceous (Cenomanian) ; England.

REMARKS. The processes are commonly acuminate, often joining proximally, but may be branched. Only rarely can any alignment of these processes be observed. The apical process makes orientation easy and indicates that the archaeopyle is precingular. Detached archaeopyle plates have been found and these show the characteristic precingular shape.

Exochosphaeridium phragmites sp. nov.

Pl. 2, figs. 8—10

DERIVATION OF NAME. Latin, *phragmites*, a reed—with reference to the reed-like shape of the processes of this species.

DIAGNOSIS. Central body subspherical to oval, possessing a pitted surface and bearing numerous acuminate processes. Processes solid or fibrous, broad-based, bases of adjacent processes often confluent. Distinctively branched apical process present and commonly a precingular archaeopyle.

HOLOTYPE. Geol. Surv. Colln. PF.3035(3). Lower Chalk, H.M. Geological Survey Borehole, Fetcham Mill, Surrey at 840 ft. depth. Upper Cretaceous (Cenomanian).

PARATYPE. Geol. Surv. Colln. PF.3043(1). H.M. Geological Survey Borehole, Fetcham Mill, Surrey at 810 feet depth. Upper Cretaceous (Cenomanian).

DIMENSIONS. Holotype : diameter of central body 49 by 56 μ , length of processes up to 22 μ . Paratype : diameter of central body 33 by 36 μ , length of processes up to 22 μ .

DESCRIPTION. The fibrous processes may occasionally be slightly perforate. Division of a process into two often takes place medially, and more rarely distally. The processes may terminate distally in a point or may be blunted. The arrangement of the processes usually appears to be haphazard and in only one specimen, the paratype, can any alignment be observed. In this specimen a definite alignment can be seen on both sides of the cingulum running parallel to this structure. An apical process and an archaeopyle are present, thus making orientation easy. The apical process is very distinctive, being foliate in shape ; it is situated near the edge of the archaeopyle. The position of this process indicates that it must be an apical process and that the archaeopyle is precingular. *E. phragmites* occurs throughout the Cenomanian of England.

REMARKS. Superficially *E. phragmites* resembles *Baltisphaeridium striolatum* Deflandre, the holotype of which was examined by one of the authors (R.J.D.) by kind permission of Professor Deflandre. *B. striolatum*, however, has a definitely striated periphragm on the surface of the central body and neither a distinctive apical process nor an archaeopyle has been observed. It must be made clear, however, that the holotype of *B. striolatum* is extremely dark and the lower surface, which may possess an archaeopyle and an *apical* process, is not observable.

OTHER SPECIES

The following species are here included in *Exochosphaeridium* gen. nov. on the basis of similarity in structure and process pattern :

Exochosphaeridium palmatum (Deflandre & Courteville 1939). Upper Cretaceous ; France.

Exochosphaeridium striolatum (Deflandre 1937a). Upper Cretaceous ; France.

The following species is tentatively referred to this genus, subject to subsequent confirmation of the precingular position of the archeopyle :

?*Exochosphaeridium pseudhystrichodinium* (Deflandre 1937a). Upper Cretaceous ; France.

Genus **CLEISTOSPHAERIDIUM** nov.

DERIVATION OF NAME. Greek, *kleistos*, shut, closed ; *sphaera*, ball—in reference to shell shape and the closed nature of the processes.

DIAGNOSIS. Chorate dinoflagellate cysts having spherical to ovoidal central bodies bearing numerous processes, typically closed distally and without communication to endocoel. Number of processes typically exceeding 50 ; processes showing no definite alignment, so that the tabulation is not determinable. Archaeopyle apical, with zigzag margin.

TYPE SPECIES. *Cleistosphaeridium diversispinosum* sp. nov. Eocene ; England.

REMARKS. It is not clear whether the processes of this genus are intertabular or intratabular ; nor is there any differentiation between processes which would enable the establishment of orientation. The shape and size of the archaeopyle, however, strongly suggests that it is apical.

All Mesozoic and Tertiary species, formerly attributed to *Baltisphaeridium*, which show an apparent apical archaeopyle and which cannot be related to *Surculosphaeridium* or *Prolixosphaeridium*, are provisionally reattributed to this genus. Species are included whose process numbers are relatively low ; it is probable that re-examination of these will necessitate their removal to other genera as soon as the reflected tabulation is determined.

Cleistosphaeridium diversispinosum sp. nov.

Pl. 10, fig. 7

DERIVATION OF NAME. Latin, *diversus*, different; *spinosus*, thorny—with reference to the variable shape of the processes.

DIAGNOSIS. A *Cleistosphaeridium* with granular wall and polygonal archaeopyle. Processes solid, taeniate or tubular, usually slender and proximally expanded. Distal end forked or expanded.

HOLOTYPE. B.M.(N.H.) slide V.51750(1). Eocene (London Clay); Whitecliff.

DIMENSIONS. Holotype: diameter of body 38μ , length of processes, $9-16\mu$. Observed range: diameter of body $38-43\mu$, length of processes $7-23\mu$. Number of specimens measured, 5.

DESCRIPTION. This species is distinguished by the variable nature of the process ends. The expanded termination may be bifurcate, orthogonal or patulate, one branch may be larger than the other. The edges are usually denticulate and the processes may be up to 5μ wide; but are usually about 2μ . There is more than one process to a plate.

OCCURRENCE. London Clay; Whitecliff, Enborne and Sheppey.

REMARKS. Only *Cleistosphaeridium pectiniforme* (Gerlach) 1961 comb. nov. resembles *C. diversispinosum* to any degree. It has widely forked processes with spinose margins; it does not, however, have the variability of process ending shown by our species. The species *pectiniforme* is reattributed to the genus *Cleistosphaeridium* provisionally on the basis of its similarity to *C. diversispinosum*, despite lack of knowledge of its mode of archaeopyle formation.

Cleistosphaeridium ancoriferum (Cookson & Eisenack)

Pl. 9, fig. 1

1960a. *Hystriosphæridium ancoriferum* Cookson & Eisenack: 8, pl. 2, fig. 11.

1964. *Hystriosphæridium ancoriferum* Cookson & Eisenack; Cookson & Hughes: 47, pl. 9, fig. 7.

DESCRIPTION. The specimens of *C. ancoriferum* found in the Lower Cenomanian of England, first described and figured by Cookson & Hughes (1964) strongly resemble those examples recorded from Australia (Cookson & Eisenack, 1960a). Many of the specimens from the Fetcham Mill Borehole possess a 6-sided apical archaeopyle the shape of which is often difficult to determine due to distortion. However, detached apical regions are relatively abundant. The processes are hollow, the cavity often being constricted to some extent, and closed distally and proximally. They do not appear to be aligned to any noticeable extent.

C. ancoriferum has been recorded from the Albian and Cenomanian of England and Australia.

MATERIAL (figured). Geol. Surv. Colln. slide PF.3044(1). Lower Chalk, H.M. Geological Survey Borehole, Fetcham Mill, Surrey, at 810 feet depth. Upper Cretaceous (Cenomanian).

DIMENSIONS. Figured specimen : diameter of central body 32 by 41μ , length of processes up to 9μ . Range : diameter of central body 20– 45μ , length of processes up to 9μ . Number of specimens measured, 30.

REMARKS. As with Cookson & Hughes (1964), difficulty was met with when trying to distinguish *C. ancoriferum* from *Chlamydophorella nyei* (Cookson & Eisenack 1958), since the outer membrane and apical prominence of the latter are often obscure. The processes of *C. nyei*, however, are finer and shorter than those of *C. ancoriferum*.

Cookson & Eisenack (1960a) comment on the "transparent tips" of the processes of *C. ancoriferum*. The cavities are in fact closed by a thin, transparent membrane. This character may well indicate a close relation to *Chlamydophorella*. The species *Cleistosphaeridium ancoriferum* may have arisen by the progressive restriction of a formerly continuous membrane ; or alternatively, *Chlamydophorella* may have arisen by the extension of a membrane which originally merely tipped the processes.

***Cleistosphaeridium heteracanthum* (Deflandre & Cookson)**

Pl. 2, figs. 6, 7

1955. *Hystrichosphaeridium heteracanthum* Deflandre & Cookson : 276, pl. 2, figs. 5, 6 ; text-figs. 40, 41.

1961a. *Hystrichosphaeridium heteracanthum* Deflandre & Cookson ; Cookson & Eisenack : 73, pl. 12, fig. 14.

1963. *Baltisphaeridium heteracanthum* (Deflandre & Cookson) Downie & Sarjeant : 91.

REMARKS. The Cenomanian specimens from England are very similar to the forms illustrated by Deflandre & Cookson (1955) from the Upper Cretaceous of Victoria, Australia.

The surface of the central body may be smooth or reticulate. The processes are extremely variable in shape but do not vary markedly in length. One complete specimen has been found and this possessed one large distinctive process. In all the other studied examples this process was absent and there was, in every case, a large, well defined, archaeopyle. It is probable, therefore, that the process is apical and that the archaeopyle, when developed, is also apical in position. Alignment of the processes on the surface of the central body has not been observed. Some difficulty was experienced in distinguishing *C. heteracanthum* from *C. multifurcatum* (Deflandre). The processes of the latter, however, appear to be considerably less varied, most of them terminating with a simple bifurcation or being blunted.

C. heteracanthum is found throughout the Cenomanian of England, and in Australia it has been recorded from the Upper Cretaceous and Lower Eocene.

One specimen of *C. heteracanthum* illustrated by Deflandre & Cookson (1955, pl. 12, fig. 14) appears to possess an apical archaeopyle. For the latter reason this species is tentatively placed in the genus *Cleistosphaeridium*.

MATERIAL (figured). Pl. 2, fig. 6, Geol. Surv. Colln. slide PF.3041(2). Lower Chalk, H.M. Geological Survey Borehole, Fetcham Mill, Surrey, at 650 feet depth. Upper Cretaceous (Cenomanian). Another specimen, Pl. 2, fig. 7, at 840 feet depth.

DIMENSIONS. Figured specimens : diameter of central body 52 by 59 μ , length of processes up to 17 μ . Range of Cenomanian specimens : diameter of central body 50–68 μ , length of processes up to 17 μ . Number of specimens measured, 5.

?Cleistosphaeridium flexuosum sp. nov.

Pl. 2, fig. 5

DERIVATION OF NAME. Latin, *flexuosus*, flexuous—with reference to the form of the processes.

DIAGNOSIS. Central body subspherical to elongate, bearing numerous, broadly acuminate, processes. All processes of approximately same length, slightly fibrous and always flexuous.

HOLOTYPE. Geol. Surv. Colln. slide PF.3045(1). Lower Chalk, H.M. Geological Survey Borehole, Fetcham Mill, Surrey at 840 feet depth. Upper Cretaceous (Cenomanian.)

DIMENSIONS. Holotype : diameter of central body 29 by 37 μ , length of processes up to 17 μ . Range : diameter of central body 20 to 45 μ , length of processes up to 20 μ . Number of specimens measured, 4.

DESCRIPTION. The most distinctive feature of ?*C. flexuosum* is the flexuous nature of the broad fibrous processes. The nature of the surface of the central body is difficult to determine and the presence of an archaeopyle has not been recorded.

This is a rare species throughout the Cenomanian of England.

REMARKS. The nature of the processes easily differentiate ?*C. flexuosum* from all previously described species. This species is tentatively placed in *Cleistosphaeridium* on the general form of the central body and processes.

Cleistosphaeridium disjunctum sp. nov.

Pl. 11, fig. 9

DERIVATION OF NAME. Latin, *dis*, asunder ; *junctus*, joined.

DIAGNOSIS. A *Cleistosphaeridium* with granular central body and polygonal archaeopyle. Numerous processes hollow, unbranched, closed distally and proximally, with distal terminations blunt, acuminate, or bearing small spines. Processes regularly arranged.

HOLOTYPE. B.M.(N.H.) slide V.51739(2). Eocene (London Clay) ; Whitecliff.

DIMENSIONS. Holotype : diameter of central body 47–54 μ , length of processes 10–15 μ . Observed range : diameter of body 30–56 μ , process length 10–19 μ . Number of specimens measured, 13.

DESCRIPTION. Attempts to make subdivisions on the type and pattern of processes have been fruitless ; the species is a very variable one. The wall also shows considerable variation in thickness.

The processes are from a quarter to a half of the body diameter and are hollow. The process length in an individual is constant, as are the process terminations. The number of processes exceeds 50. Plates can be recognized on damaged specimens and the number of processes ranges from four to seven on each plate.

OCCURRENCE. London Clay ; Whitecliff and Enborne.

REMARKS. *C. disjunctum* resembles *Baltisphaeridium densicomatum* (Maier) which however splits equatorially and sometimes has forked processes. *B. iaculigerum* Klement has longer processes and the archaeopyle is unknown.

In view of the regular arrangement of the processes, a feature not typical of the genus, the allocation of this species to *Cleistosphaeridium* must be regarded as provisional.

OTHER SPECIES

The following species, formerly attributed to *Baltisphaeridium*, are here provisionally reattributed to *Cleistosphaeridium* gen. nov., on the basis of their apparent possession of an apical archaeopyle and in absence of knowledge of their reflected tabulation (if any). Species of especially doubtful character are differentiated with a question mark :

Cleistosphaeridium ashdodense (Rossignol 1962). Miocene ; Australia.

?*Cleistosphaeridium danicum* (W. Wetzel 1952). Paleocene (Danian) ; Baltic.

Cleistosphaeridium echinoides (Maier 1959). Oligocene ; Germany.

Cleistosphaeridium ehrenbergi (Deflandre 1947b). Upper Jurassic ; France.

Cleistosphaeridium israelianum (Rossignol 1962). Quaternary ; Israel.

Cleistosphaeridium leve (Maier 1959). Oligocene-Miocene ; Germany.

Cleistosphaeridium lumectum (Sarjeant 1960a). Upper Jurassic ; England.

Cleistosphaeridium machaerophorum (Deflandre & Cookson 1955). Miocene ; Australia.

Cleistosphaeridium multifurcatum (Deflandre 1937a). Upper Cretaceous ; France.

?*Cleistosphaeridium oligacanthum* (W. Wetzel 1952). Paleocene (Danian) ; Baltic.

Cleistosphaeridium pectiniforme (Gerlach 1961). Oligocene ; Germany.

Cleistosphaeridium pilosum (Ehrenberg 1954). Upper Jurassic ; Poland.

Cleistosphaeridium polytrichum (Valensi 1947). Middle Jurassic ; France.

?*Cleistosphaeridium spiralisetum* (de Wit 1943). Upper Cretaceous ; Netherlands.

Cleistosphaeridium tiara (Klumpp 1953). Eocene ; Germany.

Cleistosphaeridium tribuliferum (Sarjeant 1962b). Upper Jurassic ; England.

Genus ***PROLIXOSPHAERIDIUM*** nov.

DERIVATION OF NAME. Latin, *prolixus*, stretched out long ; *sphaera* ball—with reference to the shape of the central body.

DIAGNOSIS. Shell shape elongate ovoidal to ellipsoidal, one pole (apical) typically lost in archaeopyle formation. Opposite pole occupied by one or two antapical processes. Remaining processes arranged in distinct rows encircling test ; these rows slightly offset at a position corresponding to sulcus. Number of processes exceeding 30. Processes closed proximally, closed or open distally : their distal terminations simple ; flaring in varied fashion ; or briefly furcate. Shell surface bearing cover of coarse granules or very short, simple spinelets, or lacking such ornamentation.

TYPE SPECIES. *Prolixosphaeridium deirense*, sp. nov. Lower Cretaceous (Middle Barremian) ; England.

REMARKS. A group of Mesozoic dinoflagellate cysts exhibit an elongate central body with a terminal archaeopyle. Their distinctive character and unity of form merits taxonomic recognition at generic level. The arrangement of the processes suggests that they are intratabular, corresponding perhaps to crest nodes, but prolonged study of many individuals would be necessary before this could be confirmed.

Prolixosphaeridium deirense sp. nov.

Pl. 3, fig. 2 ; Text-fig. 45

DERIVATION OF NAME. Latin, *deirense*, of Deira, the ancient kingdom occupying what is now East Yorkshire.

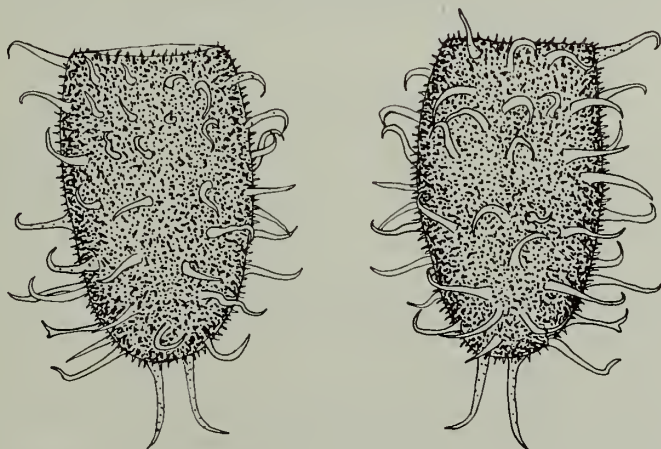


FIG. 45. *Prolixosphaeridium deirense* gen. et sp. nov. Left, ventral view ; right, dorsal view. $\times$ c. 1000.

DIAGNOSIS. A *Prolixosphaeridium* having an elongate ovoidal central body bearing 60–65 processes. Processes simple or briefly bifurcate (bifurcations unequally long), closed proximally, dominantly or constantly closed distally. Two processes occupying antapical pole; remaining processes showing alignment in rows, encircling test and offset at a position corresponding to sulcus. Apex typically lost in archaeopyle formation; about six rows of processes present between archaeopyle and antapex, gap between third and fourth row probably corresponding to cingulum. Test surface granular and bearing dense cover of very short spinelets.

HOLOTYPE. B.M.(N.H.) slide V.51727(2), Speeton Clay, Shell West Heslerton boring, Yorkshire, Lower Cretaceous (Middle Barremian).

DIMENSIONS. Holotype: overall length (apex lacking) 62μ ; overall breadth 46μ ; shell length (apex lacking) 50μ ; breadth 28μ ; spines c. 10 – 12μ long, spinelets 1 – 1.5μ long. Dimensions of other specimens closely similar.

DESCRIPTION. The distribution of the processes on the epitheca is into three rows; these appear to respectively comprise 9, 10 and 10 processes. Distribution of processes on the hypotheca was less easily determined. Two rows of processes were present posterior to the presumed cingulum, each apparently comprising 9 processes; and some 9 further processes clustered round the antapex, probably but not certainly representing a sixth process row.

The short spinelets form a stubble on the granular surface of the periphragm.

REMARKS. This species was encountered only in the 39 foot horizon in the West Heslerton Borehole. It closely resembles the Upper Jurassic species *P. mixtispinosum* (Klement 1960), differing in the broader shell shape (length-width ratio of *P. mixtispinosum* consistently greater than 2 : 1, against a length-width ratio in *P. deirense* consistently markedly less than 2 : 1); in the furcate character of some processes; and in the somewhat shorter spinelets. These distinctions are minor; there can be no doubt that *P. deirense* and *P. mixtispinosum* are closely related.

Prolixosphaeridium granulosum (Deflandre)

- 1937. *Hystrichosphaeridium xanthiopyxides* var. *granulosum* Deflandre : 29, pl. 16, fig. 4.
- 1955. *Hystrichosphaeridium xanthiopyxides* var. *granulosum* Deflandre; Valensi : 594, pls. 3, fig. 7, pl. 5, fig. 16.
- 1957. *Hystrichosphaeridium xanthiopyxides* var. *granulosum* Deflandre; Downie : 426, text-fig. 46.
- 1960. *Baltisphaeridium xanthiopyxides* var. *granulosum* (Deflandre) Klement : 59,
- 1962a *Baltisphaeridium granulosum* (Deflandre); Sarjeant : 264, pl. 2, fig. 14, text-fig. 8c.

REMARKS. This species, which has a known range from Upper Jurassic to Upper Cretaceous, is represented in the London Clay at Whitecliff and Enborne; it is, however, possible that these specimens are derived.

It differs from *P. deirense* in having only approximately 30 processes, organized into rows, with one antapical process.

OTHER SPECIES

The following species are here included in the genus *Prolixosphaeridium* nov., on the basis of shape, character of processes and possession of an apical archaeopyle :

Prolixosphaeridium mixtispinosum (Klement 1960). Upper Jurassic ; Germany.

Prolixosphaeridium parvispinum (Deflandre 1937a). Upper Cretaceous ; France.

The following species, inadequately described and figured, is doubtfully referred to this genus :

?*Prolixosphaeridium xanthiopyxides* (O. Wetzel 1933). Upper Cretaceous ; Germany.

OTHER MESOZOIC AND CAINOZOIC SPECIES ATTRIBUTED TO *BALTISPHAERIDIUM*

In the preceding section, the bulk of post-Palaeozoic species, hitherto placed in *Baltisphaeridium*, have been reattributed to four new genera on the bases of shape, process arrangement and possession of archaeopyles. The species *Baltisphaeridium spinosum* (White) is considered in the previous chapter ; it is shown to be probably synonymous with *Hystrichodinium pulchrum* Deflandre but since the holotype of *B. spinosum* is lost, restudy is not possible. The abandonment of the name *spinosum* is therefore proposed. The species *Baltisphaeridium geometricum* (Pastiels) was originally placed in the genus *Hystrichosphaeridium* and was then a junior homonym of a species proposed by Deflandre (1945) ; since invalid at the time of publication, this name must be rejected. Pastiel's forms are attributable to the genus *Wetzelietta* and are discussed more fully on p. 192.

The holotypes of the two species, *Baltisphaeridium ferox* (Deflandre) and *B. tri-dactylites* (Valensi) were re-examined recently by one of the authors (R.J.D.) in consultation with Prof. Deflandre. On the basis of this re-examination, their reattribution to *Hystrichokolpoma* is here proposed. Reattribution of two species, (*Baltisphaeridium neptuni* Eisenack 1958 and *B. triangulatum* Gerlach 1961) to the genus *Achomosphaera* is proposed on pp. 51, 52 ; and in the discussion of the genus *Hystrichosphaeridium* and its allies (see pp. 53-105) the reattribution of two further species to new genera is proposed, *Baltisphaeridium dictyophorum* (Cookson & Eisenack) becoming *Oligosphaeridium* and *B. striatoconus* (Deflandre & Cookson) becoming *Litosphaeridium*.

Five further species currently attributed to the genus *Baltisphaeridium* appear also to merit reattribution. Four species from the German Tertiary, three of them attributed by Maier (1959) to her invalid genus *Galea* and subsequently reattributed by Downie & Sarjeant (1963) to *Baltisphaeridium* (*B. galea* ; *B. lychnum* ; *B. rehdense* ; and *B. twistringense*) are herewith tentatively reattributed to the genus *Areoligera* on the basis of archaeopyle structure. The species *Baltisphaeridium placacanthum* (Deflandre & Cookson) is herewith reattributed to *Systematophora*, since the processes show the grouping characteristic of the latter genus.

A residue of Mesozoic and Tertiary species remain, which either appear definitely acritarchs or whose morphology is not at present sufficiently well known for any

retribution to be made. These are, for the time being, left in the genus *Baltisphaeridium* ; they are as follows :

- Baltisphaeridium armatum* (Deflandre, 1937) Downie & Sarjeant 1963. Upper Cretaceous ; France.
- B. asteroides* (Maslov 1956) Downie & Sarjeant 1963. Upper Cretaceous ; Caucasus, U.S.S.R.
- B. clavicolorum* (Deflandre 1938) Downie & Sarjeant 1963. Upper Jurassic ; France.
- B. clavispinulosum* Churchill & Sarjeant 1963. Quaternary ; Australia.
- B. densicomatum* (Maier 1959) Gerlach 1961. Oligocene ; Germany.
- B. denticulatum* (Courteville in Deflandre 1946) Downie & Sarjeant 1963. Upper Cretaceous ; France.
- B.?* *difforme* (Pritchard 1841) Downie & Sarjeant 1963. Upper Cretaceous ; England.
- B. downiei* Sarjeant 1960a, Upper Jurassic ; England.
- B. echinoplax* Churchill & Sarjeant 1963. Quaternary ; Australia.
- B. fimbriatum* (White 1842) Sarjeant 1959. Upper Cretaceous ; England.
- B. gilsonii* (Kufferath 1950) Downie & Sarjeant 1963. Quaternary ; Belgium.
- B. horridum* (Deflandre 1937) Downie & Sarjeant 1963. Upper Cretaceous ; France.
- B. huguonioti* (Valensi 1955) Downie & Sarjeant 1963. Cretaceous ; France.
- B. intermedium* (O. Wetzel 1933) Downie & Sarjeant 1963. Upper Cretaceous ; Baltic.
- B. longofilum* (Maier 1959) Downie & Sarjeant 1963. Oligocene ; Germany.
- B. malleoferum* (White 1842) Downie & Sarjeant 1963. Upper Cretaceous ; England.
- B. mariannae* (Philippot 1949) Downie & Sarjeant 1963. Upper Cretaceous ; France.
- B. panniforme* Gerlach 1961. Oligocene ; Germany.
- B. pattei* (Valensi 1948) Sarjeant 1960a. Middle Jurassic ; France.
- B. paucifurcatum* (Cookson & Eisenack 1961b) Downie & Sarjeant 1964. Eocene ; Australia.
- B. pectiniforme* Gerlach 1961. Oligocene ; Germany.
- B. plicatum* (Maier 1959) Downie & Sarjeant 1963. Oligocene ; Germany.
- B. (?) polyceratum* Takahashi 1964. Oligocene ; Japan.
- B. polyozon* Brosius 1963. Oligocene ; Germany.
- B. quaternarium* Churchill & Sarjeant 1963. Quaternary ; Australia.

- B. saturnium* (Maier 1959) Downie & Sarjeant 1963. Miocene ; Germany.
- B. seminudum* (W. Wetzel 1952) Downie & Sarjeant 1963. Paleocene (Danian) ; Baltic.
- B. spiculatum* (White 1844) Downie & Sarjeant 1963. Upper Cretaceous ; England.
- B. stimuliiferum* (Deflandre 1938) Sarjeant 1960c. Upper Jurassic ; France.
- B. sylheti* (Baksi 1963) Downie & Sarjeant 1964. Eocene ; Assam, India.
- B. telmaticum* Churchill & Sarjeant 1963. Quaternary ; Australia.
- B. tinglewoodense* Churchill & Sarjeant 1963. Quaternary, Australia.
- B. varispinosum* Sarjeant 1959. Middle Jurassic ; England.
- B. whitei* (Deflandre & Courteville 1939) Downie & Sarjeant 1963. Upper Cretaceous ; France.

It is apparent, from illustrations and descriptions, that the bulk of these species will be demonstrated in the future also to be the cysts of dinoflagellates ; acritarchs appear relatively infrequent after the Palaeozoic. Five of the species listed are freshwater forms from the Australian Quaternary ; a restudy of their taxonomy is in progress.

VIII. THE GENUS *HYSTRICHOKOLPOMA*

By G. L. WILLIAMS & C. DOWNIE

INTRODUCTION

The appearance of *Hystrichokolpoma* makes it one of the most striking of the Tertiary dinoflagellate cysts. It occurs in small numbers throughout the London Clay where its excellent preservation enables the tabulation to be determined completely in many circumstances. Two previously described and one new species are recorded.

Genus *HYSTRICHOKOLPOMA* Klumpp 1953 : 388

EMENDED DIAGNOSIS. Chorate cysts bearing two types of intratabular processes, large types with expanded bases, and slender ones. Large processes have proximally a quadrate cross section reflecting plate outline. Slender processes delimiting well marked cingular and sulcal zone. Cingulum helicoid. Reflected tabulation of 4', 6", 6g, 5''', 1p, 1'''. Archeopyle apical tetratabular.

TYPE SPECIES. *Hystrichokolpoma cinctum* Klumpp 1953. Eocene ; Germany.

DISCUSSION. *Hystrichokolpoma* is a genus with a spherical to ellipsoidal central body possessing intratabular processes, radial symmetry and an apical archeopyle. Each large process almost completely occupies a single plate proximally assuming the outline of the plate leaving only a narrow border all round. Distally these processes taper and may be open or closed. They are restricted to the apical, precingular, postcingular, antapical and commonly anterior sulcal plates. The antapical plate is easily recognizable, having a longer process than the others. The slender processes are restricted to the cingular and sulcal zones. The number of equatorial processes per plate is constant in an individual but can vary within the species as now defined (personal communication from Dr. W. R. Evitt). The apical plates are rarely found in position. Breakage along sutures readily occurs when attempting to mount specimens of *Hystrichokolpoma*. Process variation in structure and number is considerable and needs careful study.

Hystrichokolpoma eisenacki sp. nov.

Pl. 17, figs. 1-3 ; Text-fig. 46

1954. *Hystrichokolpoma cinctum* Klumpp ; Eisenack : 64, pl. 10, figs. 11-14.

DERIVATION OF NAME. After Prof. Alfred Eisenack, pioneer worker on fossil dinoflagellates.

DIAGNOSIS. Ellipsoidal central body with wall composed of two closely appressed layers—the smooth or granular endophragm and the thinner smooth periphragm. Endophragm continuing uninterrupted beneath processes formed from periphragm.

Processes of two types, large ones with quadrate bases, cylindrical or tapering with open ends, and small slender processes, with ends open or closed. Antapical process much longer than others. Tabulation typical for genus. Number of slender processes on each cingular plate limited to two. Cingulum helicoidal. Anterior sulcal process considerably larger than other sulcals.

HOLOTYPE. B.M.(N.H.) slide V.51958(1), London Clay; Sheppey, Kent, sample Sh. 3.

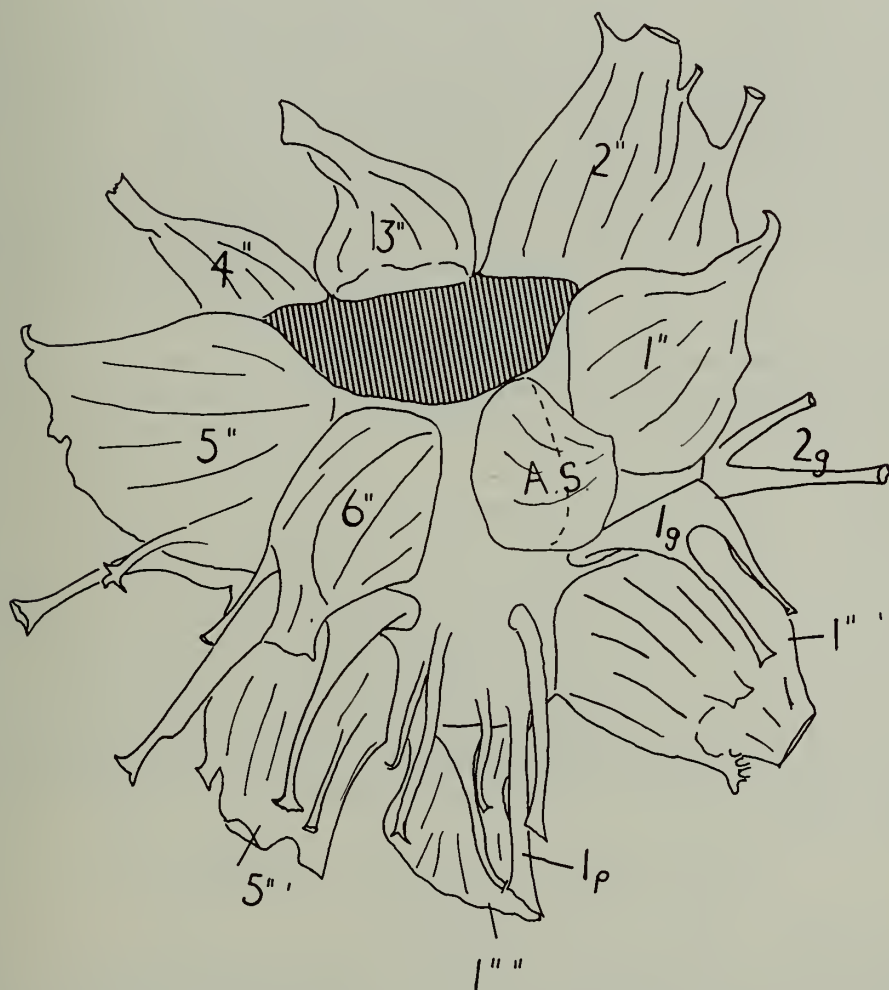


FIG. 46. *Hystrichokolpoma eisenacki* sp. nov. Ventral view of holotype showing the Tabulation. The archaeopyle is shaded.

DIMENSIONS. Holotype : diameter of central body 47 by 52 μ . Broad processes, length up to 30 μ , breadth up to 27 μ . Length of slender processes up to 22 μ . Range of dimensions observed ; diameter of central body 40–57 μ . Length of broad processes 20–30 μ . Antapical process up to 47 μ . Width of broad processes 12–27 μ . Length of slender processes 13–20 μ . Width of slender processes 0.5–4 μ . Number of specimens measured, 4.

DESCRIPTION. *H. eisenacki* is characterized by the broad processes which taper distally to a restricted opening with entire or serrate margin. Frequently branching off from the large processes are small erect tubules with an open serrate distal margin ; commonly there are three or four on each process. The equatorial processes are simple or branched, slender with slightly expanded distal openings. The four apical plates are rarely present ; the archaeopyle has a broad sulcal notch. In the precingular series of plates, plate 6'' and its attendant process are considerably smaller than the other five plates and processes, being comparable in size to the anterior sulcal plate and process. In the postcingular series, plate 1''' and its process are the smallest of the series, the other four plates and processes approaching the precingulars in size. The longest process, which tapers before expanding distally, marks the position of the single antapical plate. This process is usually closed and unbranched. There are six sulcal processes, one very large anterior process and five very slender open or bifid or acuminate processes lying between plates 1''' and 5'''. The single posterior intercalary process is little different in size and structure to the slender sulcal processes and occupies a position between 1''' and 1'''. The apical processes are usually simple, occasionally branched, tapering and open distally.

OCCURRENCE. London Clay, Whitecliff and Enborne and the Oligocene of Samland, East Prussia (Eisenack 1954).

REMARKS. The authors are indebted to Dr. W. R. Evitt of Stanford University for placing at their disposal camera lucida drawings of the holotype of *Hystri-chokolpoma cinctum* Klumpp (1953) and the originals of *H. cinctum* Klumpp of Eisenack (1954) ; they are quite different species. The drawings show that *H. eisenacki* and Eisenack's (1954) specimens of *H. cinctum* have similar tabulation and differ only in that the former has tubular branches, and not pointed spines, arising from the broad processes. Both are, however, included within the same species here named *H. eisenacki*. *H. eisenacki* differs from *H. cinctum* Klumpp (1953) in the dorsal terminations of the broad processes which are more commonly branched, the smaller number of cingular processes and the possession of a large anterior sulcal process and plate.

***Hystri-chokolpoma eisenacki* var. *turgidum* nov.**

Pl. 17, fig. 5

DERIVATION OF NAME. Latin, *turgidus*, inflated, swollen, distended.

DIAGNOSIS. Central body ovoidal slightly granular, bearing processes of two types, broad sub-conical or bulbous, with wide or restricted distal opening and slender, simple or bifurcate processes open or closed distally.

HOLOTYPE. B.M.(N.H.) slide V.51959(1). London Clay ; Enborne, sample E 11.

DIMENSIONS. Holotype : diameter of central body $40-41\mu$. Length of broad processes up to 21μ . Length of slender processes up to 24μ . Range of dimensions observed : diameter of central body $44-56\mu$. Length of broad processes $20-30\mu$, width of broad processes $8-26\mu$. Length of slender processes $16-28\mu$, width of slender processes usually $1-3\mu$. Number of specimens measured, 3.

DESCRIPTION. The broad processes of *H. eisenacki* var. *turgidum* may be sub-conical and widely open distally or bulbous with a restricted opening that has a serrate, commonly recurved, margin. Branching similar to that in *H. eisenacki* can occur, but there are rarely more than one or two branches. The longer tapering antapical process sometimes has very small tubules arising laterally and appears minutely open distally. The broad processes give rise to a characteristic trapezoid outline where they join the central body. The slender equatorial processes are variable in number, generally being restricted to two per plate, with infrequently three occurring. They are open with a digitate or serrate distal margin or they are bifurcate. Often they arise in pairs, being united proximally for as much as $\frac{1}{3}$ of their length. The tabulation is as in *H. eisenacki* with a reduced sixth precingular plate and a large anterior sulcal plate.

OCCURRENCE. London Clay ; Enborne and Sheppey.

REMARKS. *H. eisenacki* var. *turgidum* differs from *H. cinctum* in the number of cingular processes and the presence of a large anterior sulcal plate and process, and from the typical form of *H. eisenacki* in the usual presence of broad processes that have three or four branches distally.

Hystrihokolpoma unispinum sp. nov.

Pl. 17, figs. 6, 7

DERIVATION OF NAME. Latin, *uni*—one ; *spina*, spine.

DIAGNOSIS. Central body sub-spherical with thin smooth endophragm, continuous beneath processes, and thin smooth periphragm. Processes formed from periphragm and of two types, broad tapering lagenate, and buccinate more slender processes. Reflected tabulation of 4', 6'', 6g, 5''', 1p, 1'''' and at least 5s. Each cingular plate possessing only one process.

HOLOTYPE. B.M.(N.H.) slide V.51961(1), London Clay ; Whitecliff, sample WC 8.

DIMENSIONS. Holotype : diameter of central body 39 by 43μ . Length of broad processes up to 29μ , width up to 21μ . Slender processes, length up to 26μ , width up to 5μ . Range of dimensions observed : diameter of central body $39-51\mu$. Length of broad processes $21-29\mu$, breadth up to 21μ . Equatorial processes, length $18-26\mu$, breadth up to 5μ . Number of specimens measured, 3.

DESCRIPTION. The tabulation of *H. unispinum* is well shown in two specimens from the London Clay. There are four apical plates, 1' being smaller than the other three. The apical processes are tapering, open distally with a serrate or undulose margin. Five of the precingular plates and processes are equal in size, the other, plate 6'', is smaller, more closely approaching the anterior sulcal plate. The equatorial plates each possess one process. The postcingulars are as in *H. eisenacki*, with plate 1''' being reduced compared to the other four. The process of the posterior intercalary plate is small and the antapical plate is marked by a longer than average process.

The broad processes all appear open distally and may have small tubular branches. The equatorial processes are broader than in other species of *Hystrichokolpoma* and are tubiform or buccinate with serrate or undulose distal margins. A few have perforations in the wall, irregular in position. The processes may occasionally be branched. The posterior sulcal processes are slender and short with digitate endings which may be open or closed.

OCCURRENCE. London Clay ; Whitecliff and Enborne.

REMARKS. The presence of one process only on each cingular plate readily distinguishes *H. unispinum* from other species of *Hystrichokolpoma*.

Hystrichokolpoma rigaudae Deflandre & Cookson

Pl. 17, fig. 4

1954. *Hystrichokolpoma rigaudae* Deflandre & Cookson, text-fig. 15 (*n.n.*).
 1955. *Hystrichokolpoma rigaudae* Deflandre & Cookson : 279, pl. 6, figs. 6-10 ; text-fig. 42.
 1959. *Hystrichokolpoma rigaudae* Deflandre & Cookson ; Maier : 311, pl. 31, fig. 2.
 1961. *Hystrichokolpoma rigaudae* Deflandre & Cookson ; Gerlach : 183, pl. 27, figs. 8, 9.
 1962. *Hystrichokolpoma rigaudae* Deflandre & Cookson ; Rossignol : 134.
 1963. *Hystrichokolpoma rigaudae* Deflandre & Cookson ; Brosius : 43, pl. 2, fig. 6.
 1964. *Hystrichokolpoma rigaudae* Deflandre & Cookson ; Rossignol : 89, pl. 2, fig. 5, pl. 3, fig. 8.

DISCUSSION. Specimens of *H. rigaudae* from the London Clay possess a tabulation of 6'', 6c, 5''', 1p, 1'''' and 6a. Plates 6'' and 1''' and their attendant processes are reduced whilst the anterior sulcal plate is the largest of the six. A few of the broad processes and some of the girdle ones are open distally. There seems to be a degree of variability in the number of cingular processes, some plates having only one ; generally however there are two processes on each cingular plate.

DIMENSIONS. Observed range in London Clay : diameter of central body 35-48 μ . Length of broad processes up to 31 μ . Length of antapical process up to 39 μ . Number of specimens measured, 3.

OCCURRENCE. London Clay ; Whitecliff, Enborne and Sheppey. *H. rigaudae* has also been recorded from the Eocene and Miocene (or older) of Australia (Deflandre & Cookson 1954, 1955), the Middle Oligocene-Middle Miocene (Gerlach 1961), the Upper Oligocene (Brosius 1963) and the Middle Miocene of Germany (Maier 1959) and the Pleistocene of Israel (Rossignol 1962, 1964).

OTHER SPECIES

Re-examination of *Baltisphaeridium ferox* (Deflandre 1937a) Downie & Sarjeant 1963, *B. tridactylites* (Valensi 1955), Downie & Sarjeant, 1963 and *Hystrichosphaeridium clavigerum* Deflandre 1937a, by Mr. R. J. Davey and Prof. Deflandre, has determined that these species should be transferred to the genus *Hystrichokolpoma*.

The remaining species attributed to this genus are *H. sequanapartus*, Deflandre & Deflandre-Rigaud 1958, and *H. poculum* Maier 1959. A single specimen of a form very like the former was found in the London Clay.

IX. *WETZELIELLA* FROM THE LONDON CLAY

By G. L. WILLIAMS & C. DOWNIE

INTRODUCTION

The characteristic Lower Tertiary genus *Wetzeliella* is among the commonest of the London Clay dinoflagellates. The excellent state of preservation has enabled its tabulation to be determined in many instances and its resemblance to the living genus *Peridinium* is established beyond doubt. Several new forms have been discovered and it is now possible to give a fuller description of some species already named.

Genus *WETZELIELLA* Eisenack 1938 : 186

TYPE SPECIES. *Wetzeliella articulata* Eisenack 1938.

EMENDED DIAGNOSIS. Body with distinct pericoel and endocoel. Periphragm having a distinctive outline, varying from oval to pentagonal and generally prolonged into an apical horn, two lateral horns and one or two antapical horns. Periphragm may or may not bear intratabular processes. Processes (when present) open proximally, open or closed distally and frequently arranged in process complexes. Endophragm circular to ovoid in outline, in cross section biconvex and separated, by pericoel of variable size from periphragm. Reflected tabulation of 4', 3a, 7", 5'''', 2''', 3-4s, ?c not always evident. Cingulum slightly laevo-rotatory, running round maximum width of periphragm. Sulcus wider and longer on hypotract than epitract. Archaeopyle usually present in periphragm and resulting from loss of plate 2a. Endophragm usually with archaeopyle in analogous position.

DISCUSSION. *Wetzeliella* is related to the living genus *Peridinium*, since it possesses identical tabulation and the same type of archaeopyle. It is distinguishable from *Peridinium* by the presence of usually well developed lateral horns, and in most cases by the numerous processes on the pericoel and the easily recognizable endocoel. Eisenack's (1964) placing of *Wetzeliella* and *Deflandrea* in a separate sub-order from *Peridinium* appears to be an artificial classification which disregards the evidence of tabulation. *Dracodinium* Gocht, 1955, is no longer recognized as a separate genus, since all stages of transition from *Dracodinium solidum*, the sole species of the genus, to *Wetzeliella similis* (Eisenack) occur in the London Clay. *D. solidum* (pars) is therefore placed in the genus *Wetzeliella*. Gocht's statement that the position of the slip hole (archaeopyle) is variable, prevents the complete incorporation of *Dracodinium solidum* in *Wetzeliella*. Two sub-genera of *Wetzeliella* are recognized, *Wetzeliella* (*Wetzeliella*) Eisenack and *Wetzeliella* (*Rhombodinium*) (Gocht) Alberti, 1961.

The tabulation, which in many species is hard to determine, has been worked out for *W. articulata*, *W. clathrata* Eisenack, *W. coleothrypta* sp. nov., *W. reticulata* sp. nov. *W. tenuivirgula* sp. nov., *W. homomorpha* Deflandre & Cookson 1955, *W. condylos* sp. nov., and *W. similis* Eisenack 1954. In the sub-genus *Wetzeliella* (*Rhombodinium*) usually the only guide to tabulation is the archaeopyle.

Sub-genus *Wetzeliella* (*Wetzeliella*) Eisenack 1938.

DIAGNOSIS. A sub-genus of the genus *Wetzeliella*, possessing numerous processes developed from the periphragm. Processes showing only moderate variation in length and may be united distally. Processes intratabular, forming simulate complexes, or haphazardly distributed on plate.

TYPE SPECIES. *Wetzeliella* (*Wetzeliella*) *articulata* Eisenack 1938.

***Wetzeliella* (*Wetzeliella*) *articulata* Eisenack**

Pl. 18, figs. 1-4

1935. *Peridinium* sp., O. Wetzel : 168, pl. 2, fig. 1.
 1938. *Wetzeliella articulata* Eisenack : 186, text-fig. 4.
 1950. *Wetzeliella articulata* Eisenack ; Reissinger : 119, pl. 19, fig. 6.
 1952. *Wetzeliella articulata* Eisenack ; Gocht : 314, pl. 2, figs. 38, 39.
 1952. *Wetzeliella articulata* Eisenack ; Deflandre, text-fig. 89.
 1953. *Wetzeliella articulata* Eisenack ; Klumpp : 393, pl. 19, figs. 1-5.
 1954. *Wetzeliella articulata* Eisenack ; Eisenack : 55, pl. 7, figs. 1-11 ; pl. 8, figs. 14-16.
 1956. *Wetzeliella articulata* Eisenack ; Cookson : 185, pl. 2, fig. 6.
 1959a. *Wetzeliella articulata* Eisenack ; Eisenack, pl. 3, fig. 7.
 1961. *Wetzeliella articulata* Eisenack ; Evitt : 397, pl. 8, figs. 3, 5, 6.
 1961. *Wetzeliella articulata* Eisenack ; Gerlach : 152, pl. 25, fig. 2.

DISCUSSION. *W.* (*W.*) *articulata* is of widespread occurrence in the London Clay of Enborne and Sheppey but is uncommon at Whitecliff. The London Clay specimens do not vary from the type material. The tabulation has been worked out in a few individuals, from the alignment of some of the intratabular processes in simulate complexes. These are four apicals, three anterior intercalaries (of which plates 1a and 3a are elongate) ; seven precingulars (with plates 2" and 6" elongate) ; 5 post-cingulars (all well developed plates) ; two antapicals of approximately equal size and three sulcals, with the posterior sulcal plate the largest. That the endophragm is subdivided into plates of similar orientation is suggested by the regularly orthogonal outline of the inner archaeopyle.

Of the two antapical horns always present in *W.* (*W.*) *articulata* the longer invariably lies to the right of the mid-ventral line, (for definition see Evitt 1963). The processes forming the simulate complexes lie just in from the plate boundaries. A few of the London Clay specimens have granular processes. Beautifully formed crystals of pyrite are found in the horns of some specimens but only rarely in the endocoel.

Specimens intermediate to *Wetzeliella symmetrica* Weiler (1956) from the Oligocene of Germany, are not uncommon in the London Clay. These possess a reduced left antapical horn and/or an elongate apical horn, a length/breadth ratio of approximately 1 to 1 and are probably synonymous with *W.* cf. *symmetrica* (Weiler) Maier (1959). Gerlach (1961) in a discussion of *W. symmetrica symmetrica* Weiler, mentions the occurrence of specimens with a second antapical horn. Unfortunately she did not figure any such types.

Other individuals having a reduced apical horn and sometimes also a poorly developed left antapical horn are intermediate to *W. similis* Eisenack. These are of less frequent occurrence than the previously described forms.

The forms recorded by Pastiels (1948) as *Hystrichosphaeridium articulatum* and transferred to *W. articulata* by Eisenack (1954), are not in fact representatives of this latter species. The diagnostic characteristics of *W. articulata* are the possession of a well developed apical horn and two well developed antapical horns, usually unequal in size. Pastiels' forms do not have this well developed second antapical horn and are transferred to *W. (W.) symmetrica* var. *lobisca* (see p. 196).

DIMENSIONS. Observed range in London Clay : outer shell length 111–162 μ , breadth 64–105 μ . Number of specimens measured, 28.

OCCURRENCE. Eocene, London Clay ; Whitecliff, Studland, Sheppey and Enborne. *W. articulata* has been recorded in Europe from the Lower Eocene to the Middle Miocene.

***Wetzeliiella (Wetzeliiella) articulata* var. *conopia* nov.**

Pl. 18, fig. 5

DERIVATION OF NAME. Greek, *konopos*—gnat.

HOLOTYPE. B.M.(N.H.) slide V.51962. London Clay ; Sheppey, Kent, sample SL.4.

DIMENSIONS. Holotype : outer shell length 132 μ , breadth 126 μ , Capsule length 88 μ . Observed range : outer shell, length 120–156 μ . Capsule, length 88–105 μ , breadth 83–92 μ . Number of specimens measured, 4.

DESCRIPTION. A variety of *W. (W.) articulata* having processes that distally may give rise to long aculei, often interconnected with aculei of adjacent processes. This is an intermediate form to *W. (W.) leptavirgula* sp. nov. It has been found in the London Clay only at Sheppey.

***Wetzeliiella (Wetzeliiella) clathrata* Eisenack**

Pl. 18, fig. 6

1938. *Wetzeliiella clathrata* Eisenack : 187, text-fig. 5.

1954. *Wetzeliiella clathrata* Eisenack ; Eisenack : 57, pl. 7, figs. 12–14 ; text-fig. 2.

1961. *Wetzeliiella clathrata* Eisenack ; Gerlach : 153, pl. 25, fig. 6.

1961. *Wetzeliiella clathrata* Eisenack ; Evitt : 397, pl. 1, fig. 19.

DISCUSSION. A single specimen from the London Clay is attributed to *W. (W.) clathrata*. Many individuals that on initial examination appear to belong to *W. clathrata* are really examples of *W. (W.) coleothrypta*. *W. clathrata* is a distinctive species whose processes are aligned in rows, immediately within the boundary of a plate, forming simulate complexes. Adjacent processes are united distally by perforate membranes restricted in width to a few microns ; these are the " lists " of Eisenack. Tabulation is as in *W. articulata* and the reduced antapical horn lies to the left of the mid-ventral line.

Wetzeliella (Wetzeliella) coleothrypta sp. nov.

Pl. 18, figs. 8, 9 ; Text-fig. 47

DERIVATION OF NAME. Greek, *koleos*, scabbard, sheath ; *thrypto*, break.

DIAGNOSIS. Thin walled periphragm characteristic pentagonal outline with each angle produced into horns, one apical, two lateral and two antapical ; left antapical horn generally reduced. Pericoel totally enclosing endophragm. Processes arising from periphragm, hollow, connecting with pericoel. Distally processes of individual simulate complex united by finely perforate membrane assuming outline of underlying plate and extending over that plate as a replica of it. Processes commonly absent from pre- and postcingular plates on side lying nearest to cingulum. Reflected tabulation of 4', 3a, 7", 5c, 5"', 2", 3-4s.

HOLOTYPE. B.M.(N.H.) slide V.51753(3). London Clay ; Sheppey, Kent, sample Sh.4.

DIMENSIONS. Holotype : periphragm length 122μ ; breadth 110μ . Capsule length 69μ ; breadth 61.5μ . Observed range : outer shell length $112.5-157\mu$; breadth $102.5-142\mu$. Capsule length $66-106\mu$; breadth $67-97\mu$. Processes up to 15μ long. Number of specimens measured, 6.

DESCRIPTION. The periphragm of *W. coleothrypta* has an outline approaching *W. similis* on the one hand and *W. articulata* on the other. The right antapical horn is invariably longer than the left, which is often represented by a small protuberance. The apical horn has a pointed apex ; the lateral horns are indented distally due to the transverse cingulum crossing from the dorsal to the ventral surface at these two places. The slender, simple, or occasionally branched processes are intratabular,

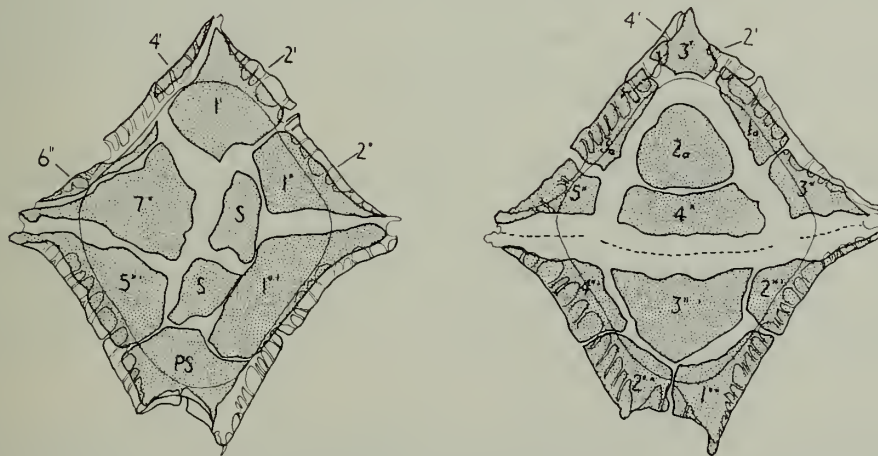


FIG. 47. *Wetzeliella (Wetzeliella) coleothrypta* sp. nov. Left, tabulation of ventral (upper) surface of holotype ; right, tabulation of dorsal (lower) surface. S, sulcal plates ; PS, posterior sulcal plate ; stippled areas show where processes are united distally by a membrane.

arising from just within the plate boundary and usually forming a simulate complex on each plate. The processes of each complex are united distally by a membrane which is finely perforate and which assumes the outline and area of the underlying plate. The general rule that the longer the processes, the further away they are from the horns, is found to be true for this species.

The plates, interpreted from the simulate complexes, show considerable variation in size. Of the apicals, plate 1' is by far the largest and has a trapezoid outline : plates 2' and 4' are lateral in position and are narrow, being represented by a single row of processes ; whilst the dorsal plate 3' is intermediate in size between 1' and 4'. The anterior intercalary plates likewise vary in size and are dorsal in position. Plates 1a and 3a are elongate, narrowing apically, whereas plate 2a, the loss of which forms the archaeopyle, is trapezoid, with processes absent from its equatorial boundary. The seven precingulars show extreme variation. Plates 1" and 7" are of comparable size with an almost triangular outline. Plates 2" and 6" are extremely narrow and are represented by a single row of processes running along the lateral margin. On the dorsal surface, the three plates 3", 4", and 5" are wider than the others and do not extend as far towards the apex, being restricted because of the anterior intercalaries. Plate 4" is the widest of the precingular series.

The circular cingulum comprises five plates, three on the dorsal surface, two on the ventral. Each plate has a single row of processes that are united distally as in *W. clathrata*. Of the postcingulars, plates 1''' and 5''' on the ventral surface are of comparable size and shape (see Fig. 47), whilst plates 2''' and 4''' are smaller though of not dissimilar outline. The widest of the postcingulars is plate 3'', which usually has no processes on the side adjacent to the transverse cingulum. This is also frequently true of most of the pre- and postcingular plates. The two antapical plates are dorsally situated. The sulcus is considerably expanded on the hypotract and extends to the distal extremities of the antapical horns. There can be three or four sulcal plates, of which the most posterior is the largest and has a rhomboidal shape. Only one sulcal plate is present on the epitract. The tabulation is always clearly shown and easily decipherable.

The width of the pericoel has no bearing on the thickness of the capsule wall, in this or any other species of *Wetzeliiella*. Thin walled capsules often lie at a considerable distance from the periphragm. Evitt's (1961c) hypothesis that the greater the distance of the capsule from the enclosing periphragm, the thicker the endophragm, must therefore be applied with caution. The capsule of *W. coleothrypta* may be slightly granular ; it possesses an archaeopyle which is in line with that of the periphragm and appears to be intercalary. The operculum of the archeopyle is often found lying within the capsule.

REMARKS. Of the described species of *Wetzeliiella*, only *W. clathrata* has processes united distally. However, whereas in *W. clathrata* the processes are united so as to give lists or bars of restricted width, in *W. coleothrypta*, the membrane assumes the outline of the plate and passes completely over it, forming an outer umbrella. The two species can therefore be easily distinguished.

Wetzelialla (Wetzelialla) reticulata sp. nov.

Pl. 19, figs. 3, 6 ; Text-fig. 48

DERIVATION OF NAME. Latin, *reticulatus*, netted, net-like.

DIAGNOSIS. Periphragm with distinctive pentagonal outline, produced into horns at each angle ; one apical, two lateral and two antapical horns. Right antapical always larger than left antapical horn. Periphragm totally enclosing ovoidal capsule. Surface of periphragm bearing intratabular processes, usually restricted to simulate complexes ; processes lying immediately within boundaries of plates. Processes diversely united within each complex by series of trabeculae, giving a reticulum extending over plate and assuming plate outline. Processes of adjacent plates not unified. Reflected tabulation 4', 3a, 7'', 5c, 5''', 2''', 3 or 4s. Archaeopyle present.

HOLOTYPE. B.M.(N.H.) slide V.51752(6). London Clay ; Sheppey, Kent, sample 2.

DIMENSIONS. Holotype : periphragm length 146μ , breadth 162.5μ , capsule length 106μ , breadth 110μ . Observed range : outer shell length 146 – 167μ , breadth 150 – 162.5μ . Capsule length 103 – 106μ , breadth 95 – 110μ . Number of specimens measured, 2.

DESCRIPTION. The shape and size of the plates of the periphragm of *W. reticulata* agree with those of *W. coleothrypta* (see previous description). The hollow, closed, cylindrical processes, in connection with the pericoel cavity are distally divided into numerous secæ which ramify and are united by means of trabeculae with secæ from processes of the same plate. The boundary of the reticulum thus formed is extremely regular, unconnected spines branching off only infrequently. Each reticulum mirrors the shape of the plate it overlies and is only slightly smaller. The trabeculae of the reticulum are taeniate.



FIG. 48. *Wetzelialla (Wetzelialla) reticulata* sp. nov. Left, tabulation of the ventral (lower) surface of holotype ; right, tabulation of the dorsal (upper) surface. Stippling denotes area of simulate process complexes. The archaeopyle in the endophragm resulting from loss of plate 2a is shaded.

Processes can arise from any point on a plate within the simulate complex, sometimes even forming secondary rows, further strengthening the reticulum.

The capsule is large, almost filling the pericoel apart from the horns. It has a thin slightly granular wall.

OCCURRENCE. Eocene, London Clay ; Sheppey.

REMARKS. *W. reticulata* has an outline closely approaching *W. articulata* which can occasionally have processes that are united distally, but never in the form of a reticulum reflecting each individual plate constituting the pericoel. *W. reticulata* differs from *W. coleothrypta* in the distal structure of the processes and in having two well developed antapical horns.

***Wetzelietta (Wetzelietta) tenuivirgula* sp. nov.**

Pl. 19, figs. 2, 4 ; Text-fig. 49

DERIVATION OF NAME. Latin, *tenuis*, thinned ; *virgula*, small twig—referring to the processes.

DIAGNOSIS. Periphragm outline pentagonal to ovoidal, with each angle produced into a well developed tapering horn—one apical, two lateral and one or two antapical. Right antapical horn always the longer.Periphragm flattened in cross section, save medially where it encloses the ovoidal capsule. Hollow, slender or branched processes arising from periphragm and arranged in simulate complexes or occurring haphazardly within complexes. Processes terminating distally in elongate, solid secæ, sometimes united to secæ of adjacent processes ; giving rise to interconnections between processes on opposite sides of plate or remaining unconnected. Tabulation typical of genus, with three sulcal plates. Archaeopyle usually formed.

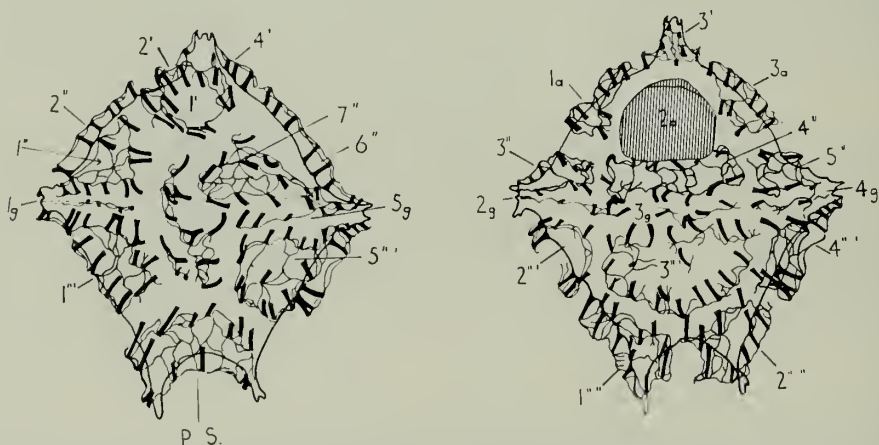


FIG. 49. *Wetzelietta (Wetzelietta) tenuivirgula* sp. nov. Left, tabulation of ventral (lower) surface of holotype ; right, tabulation of dorsal (upper) surface. Shading indicates archaeopyle.

HOLOTYPE. B.M.(N.H.) slide V.51964(2). London Clay ; Sheppey, Kent, sample 2.

DIMENSIONS. Periphragm, length $125-175\mu$; breadth $120-158\mu$. Capsule, length, $72-113\mu$; breadth $70-104\mu$. Number of specimens measured, 9.

DESCRIPTION. *W. tenuivirgula* commonly has an outline similar to that of *W. articulata*, with two well-developed antapical horns, although the left is absent in some individuals. The apical and antapical horns are acuminate distally ; the lateral horns are indented, denoting the position of a cingulum. The processes tend to be graded, being longest furthest away from the horns.

OCCURRENCE. Eocene, London Clay ; Sheppey and Enborne.

In some specimens the majority of the processes are regularly arranged just within the plate boundary and form a simulate complex ; they may also arise nearer the plate centre. The secæ, besides uniting adjacent processes, often extend across the plate, thus giving rise to a very loosely knit reticulum, totally different, in appearance to that found in *W. reticulata*. Unconnected acuminate spines, up to $2-3\mu$ in length, often arise from the interconnecting secæ or trabeculae. The trabeculae may be granular or smooth ; the secæ are usually extremely fine and regular. Processes of adjacent plates are not united. The pre- or postcingular plates may or may not have processes on the side nearest the cingulum. The capsule almost fills the pericoel, apart from the horns, and has a slightly granular wall.

W. tenuivirgula differs from *W. reticulata* in the nature of the secæ ; in the latter species these are short and complexly anastomosing and are rarely unconnected.

***Wetzeliiella (Wetzeliiella) tenuivirgula* var. *crassoramosa* nov.**

Pl. 19, figs. 1, 5, 7 ; Text-fig. 50

DERIVATION OF NAME. Latin, *crassus*, thick, stout ; *ramosus*, branching ; hence thick-branched.

HOLOTYPE. B.M.(N.H.) slide V.51954(2). London Clay ; Whitecliff, sample WC4.

DIMENSIONS. Holotype : outer shell length 125μ ; breadth 122μ . Capsule—length 80μ ; breadth 71μ . Observed range : outer shell length $125-182\mu$; breadth $122-160\mu$. Capsule, length $80-144\mu$; breadth $71-103\mu$. Number of specimens measured, 8.

DESCRIPTION. This differs from the typical *W. tenuivirgula* in the nature of the distal branching of the processes ; the secæ and trabeculae are much wider and taeniate, the reticulum being much stronger as a result. The processes forming the simulate complexes are often united by particularly wide taeniate secæ (or bars) up to 3μ in width. Frequently there are simple unconnected spines with blunt or bulbous terminations branching off from the bars and trabeculae. In outline, the outer shell lies between that of *W. articulata* and *W. symmetrica*, individuals with an outline approaching the latter species predominating.

OCCURRENCE. Eocene, London Clay ; Whitecliff.

REMARKS. *W. tenuivirgula* var. *crassoramosa* does not merit raising to specific level, on account of the frequent occurrence of forms transitional to *W. tenuivirgula*. The extreme development of the secæ (more correctly termed bars at this stage of development) however is very distinctive.

***Wetzeliiella (Wetzeliiella) homomorpha* Deflandre & Cookson**

1948. *Hystrichosphaeridium geometricum* Pastiels (pars) : 41, pl. 4, figs. 3, 5, 6, 7, 9, 10.

1955. *Wetzeliiella homomorpha* Deflandre & Cookson : 254, pl. 5, fig. 7 ; text-fig. 19.

DISCUSSION. The species *W. homomorpha* is restricted to forms having a periphragm with rhomboidal, ovoidal or sub-circular outline and which lacks well developed horns. The processes tend to be concentrated on the ambitus and are generally closed distally. The archaeopyle is intercalary. Deflandre & Cookson (1955) stated that none of the Australian examples contained the internal "cyst" characteristic of *Wetzeliiella*. Their "cyst" formed by the endophragm is in fact present in the forms from the London Clay, but is easily overlooked, since it lies close to and follows the outline of the pericoel. *W. homomorpha* is therefore a species of *Wetzeliiella* in which the periphragm and endophragm are almost in contact throughout.



FIG. 50. *Wetzeliiella (Wetzeliiella) tenuivirgula* var. *crassoramosa* nov. Tabulation of dorsal surface, showing simulate complexes.

The processes of specimens of *W. homomorpha* from the London Clay are variable, simple or branched, single or in linear complexes, distally bifid, blunt or acuminate or with restricted opening. When open the processes have an entire margin. It is impossible to distinguish varieties of *W. homomorpha* on types of processes, since different types are often found on the same individual. The tabulation agrees with that for the genus, some of the processes closely following the plate boundary and almost being on it, others being well in from the margins. The number of processes per plate is variable. The lateral, apical and antapical areas can be marked by broad multibranched processes.

Included within *W. homomorpha* are some of the forms described by Pastiels (1948) as *Hystrichosphaeridium geometricum*. Fuller discussion of the *W. homomorpha*/*H. geometricum* complex will be found under *W. homomorpha* var. *quinquelata*.

***Wetzeliiella (Wetzeliiella) homomorpha* var. *quinquelata* nov.**

Pl. 18, fig. 7

1948. *Hystrichosphaeridium geometricum* Pastiels (pars) : 41, pl. 14, figs. 1, 2, 4, 8, 11.

1961. *Wetzeliiella* cf. *ovalis* Eisenack ; Alberti : pl. 1, fig. 13.

DERIVATION OF NAME. Latin, *quinque*, five ; *latus*, side—hence, five-sided.

HOLOTYPE. B.M.(N.H.) slide V.51963(1). London Clay ; Whitecliff, sample WC4.

DIMENSIONS. Holotype : periphragm, length 94μ ; breadth 105μ . Capsule, length 69μ ; breadth 69μ . Observed range : outer shell, length (including horns and processes) $73\text{--}94\mu$, length (excluding horns and processes) $50\text{--}72\mu$, breadth (including horns and processes) $77\text{--}105\mu$, breadth (excluding horns and processes) $53\text{--}70\mu$. Capsule, length $47\text{--}69\mu$; breadth $50\text{--}69\mu$. Length of processes 7. Number of specimens measured, 7.

DESCRIPTION. This is a variety of *W. homomorpha* having a thin periphragm with a distinctly pentagonal outline. Each angle of the periphragm may be marked by a branched process, larger than the rest, or by a horn not exceeding 20μ in length. When two antapical horns are present, the right is invariably the longer. The enclosed capsule has a pentagonal outline and is closely pressed against the periphragm save at the angles. The capsule wall is usually thin and smooth.

The tabulation is often well shown from the orientation of the processes, which in some specimens are almost restricted to the plate boundary zone in simulate complexes, whilst in others they are more numerous and irregularly arranged. The hollow, simple or branched processes tend to be concentrated on the ambitus of the periphragm. As in the typical *W. Homomorpha*, the processes show considerable variation distally. They are nearly always closed with acuminate, blunt or bifid tips, but several specimens with processes that open distally with aculeate or entire

margins are included since they are identical to *W. homomorpha* var. *quinquelata* in outline, wall thickness and tendency for processes to be concentrated on the ambitus. As is to be expected, intermediate forms exist between *W. homomorpha* and *W. homomorpha* var. *quinquelata*.

OCCURRENCE. Eocene, London Clay ; Whitecliff and Enborne.

STRATIGRAPHIC RANGE. *W. homomorpha* var. *quinquelata* has previously been recorded from the Ypresian of Belgium (Pastiels 1948) and the Upper Eocene of Germany (Alberti 1961).

REMARKS. Pastiels (1948) stated that *H. geometricum* is represented by flattened capsules, roughly pentagonal, of which one of the sides, sometimes concave, is smaller. Unfortunately the name created by Pastiels was pre-occupied by *Hystri-chosphaeridium geometricum* Deflandre 1942, for forms with a polygonal test from the Palaeozoic (since transferred to *Veryhacium*). This was pointed out by Deflandre & Cookson (1955), who in erecting *W. homomorpha* compared it to *H. geometricum* (Pastiels) and concluded that the two were probably synonymous. However, in the diagnosis of *W. homomorpha*, Deflandre & Cookson stated that the theca is polygonal, more or less rounded. A detailed study of London Clay forms attributable to the *W. homomorpha*-*H. geometricum* (Pastiels) complex has shown that there are two extreme forms of common occurrence, firstly pentagonal forms, often with well developed horns, and secondly ovoidal, sub-spherical or rhomboidal forms lacking horns. The two forms can be readily separated, although intermediate types do occur.

Pastiels figured, as within his species, types identical to the two extreme London Clay forms, as well as intermediate specimens, although the holotype of *H. geometricum* (Pastiels) is almost pentagonal and the accompanying description suggests that specimens with a pentagonal outline were the more frequent in the Ypresian. It therefore seems advisable to restrict *W. homomorpha* to the forms having sub-spherical, ovoidal or rhomboidal outline, whilst defining a variety, *W. homomorpha* var. *quinquelata*, to include forms having a pericoel with pentagonal outline with or without horns. This is a workable system in the London Clay and avoids too much infra-specific variation going unheeded.

Wetzelietta (Wetzelietta) ovalis Eisenack

Pl. 18, fig. 10

1954. *Wetzelietta ovalis* Eisenack : 59, pl. 8, figs. 1-7.

DISCUSSION. The outline of the periphragm of London Clay specimens of *W. ovalis* is variable ; usually it is oval to rhomboidal, but it can be sub-pentagonal, with a fifth side tending to develop when there are two antapical horns. The angle of the sides are developed into small horns, one apical, two lateral and one or two antapical ; when there are two, the right antapical horn is always the longer. The simple or branched processes are intratabular and are uniformly present over all the surface of the pericoel, not as the type material where they are sparse on the dorsal and ventral surfaces. The tabulation of *W. ovalis* is the same as that of *W. articulata*.

The processes vary in width from $1.5-3\mu$; they are in contact with the pericoel and are distally open, their margins being aculeate, with up to six aculei arising from a single process. The length of the aculei can be as great as 7μ ; in some specimens they are granular. The nature of the processes distally is one of the diagnostic features of specimens of *W. ovalis* from the London Clay.

The capsule almost completely fills the pericoel, sometimes even exhibiting a protuberance when opposite a horn. Its wall can be smooth or granular. An archaeopyle is commonly present.

DIMENSIONS. Range observed in London Clay: outer shell—length $94-120\mu$, breadth $77-115\mu$. Capsule—length $68-79\mu$, breadth $67-78\mu$. Number of specimens measured, 7.

OCCURRENCE. Eocene, London Clay; Whitecliff and Enborne.

STRATIGRAPHIC RANGE. Present in the Oligocene of Germany (Eisenack 1954b) and in the London Clay.

Wetzelietta (Wetzelietta) condylos sp. nov.

Pl. 20, figs. 1, 2

DERIVATION OF NAME. Greek, *kondylos*, knuckle, knob, enlarged end of a bone: referring to the form of the processes.

DIAGNOSIS. Flattened outer shell with well formed lateral horns, low or absent apical horns and two antapical horns, the right one always longer. Apical area tending to be curved. Periphragm ornamented with a number of extremely short, blunt intratabular processes some arranged in simulate complexes reflecting a tabulation of 4', 3a, 7'', xc, 5''', 2''', 3s, others occurring within complexes. Hypotract of periphragm of greater length than epittract. Capsule ovoidal to sub-circular in outline ellipsoidal in cross section. Endophragm up to 3.5μ thick, surface smooth or undulating.

HOLOTYPE. B.M.(N.H.) slide V.51967. London Clay; Sheppey, Kent, sample Sh.2.

DIMENSIONS. Holotype: Periphragm, length 122μ , breadth 112.5μ . Observed range: outer shell, length $76-122\mu$, breadth $86-115\mu$. Capsule, length $56-85\mu$; breadth $62-85\mu$. Number of specimens measured, 6.

DESCRIPTION. The periphragm of *W. condylos* is up to 3μ thick and forms the extremely small processes. These open to the pericoel and are cylindrical in cross section and distally closed with a blunt ending. The height of the processes is of the order of $1-3\mu$. The characteristic generic tabulation can be determined from the regular disposition of the processes in simulate complexes on the pericoel. Auxiliary irregularly arranged processes are also common. The lateral horns of the periphragm are always prominently developed; the apical horn, if present, is at the most a small protuberance. The capsule occasionally abuts on to the inner surface of the periphragm.

OCCURRENCE. Eocene, London Clay ; Sheppey.

REMARKS. Only two described species of *Wetzeliiella*, *W. lineidentata* Deflandre & Cookson, 1955 (Lower Tertiary, Australia) and *W. irtyschensis* Alberti, 1961 (Oligocene, U.S.S.R.) have processes of a similar nature to those of *W. condylos*. *W. lineidentata* was originally based on a single damaged specimen, the apical region of which was absent. Cookson & Eisenack (1961) however, discovered beautifully preserved complete specimens of this species from the Lower Tertiary of Western Australia. *W. lineidentata* differs from *W. condylos* in having lateral horns which arise in a medial position, a hypotract and epittract of similar size, the epittract of the outer shell having a triangular outline ; the capsule outline. The two species appear to be closely related however. *W. irtyschensis* differs from *W. condylos* in having poorly developed lateral horns and two antapical horns of equal length.

Wetzeliiella (Wetzeliiella) similis Eisenack

Pl. 20, fig. 5

1954. *Wetzeliiella similis* Eisenack : 58, pl. 8, figs. 8-10.

1961. *Wetzeliiella* cf. *similis* Eisenack ; Gerlach : 154, pl. 25, fig. 5.

DISCUSSION. *W. similis* is interpreted from Eisenack's diagnosis, as a species of *Wetzeliiella* having a broad low apical horn ; long, drawn out lateral horns ; and one antapical horn, which lies to the right of the midventral line, whilst to the left the other antapical horn is represented only by a low protuberance. The figures accompanying *W. similis* in Eisenack (1954) are unfortunately too poor to give any further help in recognition of the species, although one specimen he figured (pl. 8, fig. 9) has an apical opening and must be considered to belong to a genus other than *Wetzeliiella*.

W. similis is a species intermediate between *W. articulata* and *W. solida* (Gocht) (pars) Eisenack 1961, the former having a well developed apical and two antapical horns, the latter possessing only one well developed antapical horn, whilst an apical horn is absent. Attempts to set up a varietal name of *W. similis* for forms with very reduced apical horns have proved fruitless in the London Clay, intergradation being so gradual that it is impossible to distinguish any dividing line. It is therefore considered more advisable to extend the limits of *W. similis* to include forms with apical horns less than 7μ long. Forms with apical horns below 6μ would be placed in *Wetzeliiella solida*. The apical horn of *W. similis* usually merges imperceptibly into the outline of the epittract ; it can occasionally be more sharply delimited. The single specimen described and figured by Gerlach (1961) is here included in *Wetzeliiella (W.) similis*.

Examples of *Wetzeliiella (W.) similis* from the London Clay have an apical horn which is considerably broader and lower than that of *W. articulata*, whilst the indented lateral horns are long and drawn out. The right antapical horn is always longer than the apical horn. The left antapical horn is represented by a slight bulging of the pericoel. The breadth/length ratio of the outer shell generally

exceeds 1 to 1. The slender, simple or branched processes are hollow, open distally with an aculeate margin, the aculei being patulate, orthogonal or even recurved. The processes reflect a tabulation agreeing with that of the type species *W. articulata*. The processes become shorter towards the horns. The periphragm can be up to $1/2\mu$ thick, and it is always smooth.

The capsule is ovoidal or subcircular in outline, ellipsoidal in cross section. It lies at a variable distance from the inner surface of the periphragm, and has a wall up to 2μ thick, which may be smooth or granular. Commonly observed in specimens of *Wetzeliiella* (*W.*) *similis* is a local thickening of the endophragm directly opposite the point of origin of the horns. The significance of this may be that the horns are points of weakness within the cyst.

DIMENSIONS. Outer Shell, length $100-158\mu$, breadth $117-166\mu$. Capsule, length $65-97.5\mu$, breadth $66-92\mu$. Length of processes $8-18\mu$. Number of specimens measured, 15.

OCCURRENCE. Whitecliff and Enborne.

STRATIGRAPHIC RANGE. Oligocene of Germany (Eisenack 1954) and the London Clay.

***Wetzeliiella* (*Wetzeliiella*) *solida* (Gocht) comb. nov.**

1955 *Dracodinium solidum* Gocht (pars) : 88-91, text-figs. 3a, b, 4a, b, 5a.

1961 *Wetzeliiella* (*Dracodinium*) *Solida* (Gocht) Eisenack : 306.

DISCUSSION. Only a few specimens of *W. Solida* have been recorded from the London Clay. They are characterised by the absence of an apical horn. The surface of the periphragm bear slender, simple or branched processes that distally have an aculeate margin. The processes on the ambitus of the periphragm are often the shortest. The archeopyle is intercalary, the tabulation is the same as in other species of *Wetzeliiella* with the apicals being reduced in size.

Gocht (1955) erected the genus *Dracodinium* on the single species *D. solidum* and distinguished it from *Wetzeliiella* on the absence of an apical horn. Within the species *D. solidum* he unfortunately included two distinct forms, those with intercalary archeopyles and others with an apical archeopyle. Since the emended diagnosis of *Wetzeliiella* excludes forms with an apical archeopyle, Gocht's latter type needs transferring to a new genus, whilst the forms with the intercalary archeopyle are included within the genus *Wetzeliiella* as *W. solida*.

DIMENSIONS. Periphragm, length $105-117\mu$, breadth $117.5-137\mu$. Capsule, length $68-76\mu$, breadth $69-82\mu$. Number of specimens measured, 5.

OCCURRENCE. Whitecliff and Enborne.

STRATIGRAPHIC RANGE. *W. solida* has previously been recorded from the Eocene or Oligocene? of Germany (Gocht 1955). The forms classed as *Dracodinium Solidum* by Alberti (1961, pl. 1, fig. 9) appear to be another as yet unnamed species.

Wetzeliiella (Wetzeliiella) symmetrica Weiler

Pl. 20, fig. 6

1956. *Wetzeliiella symmetrica* Weiler : 132, pl. 11, figs. 1-3 ; text-figs. 2-5.1963. *Wetzeliiella symmetrica* Weiler ; Brosius, pl. 2, fig. 7.

DISCUSSION. This species is characterized by a periphragm with rhomboidal outline, the angles of which are prolonged into more or less equally long horns. The single antapical horn sits astride the mid-ventral line. The processes commonly have aculeate distal margins or can be bifurcate.

DIMENSIONS. Range observed in London Clay : outer shell, length 125-167 μ , breadth 115-148 μ . Capsule, length 70-97 μ , breadth 66-88 μ . Number of specimens measured, 7.

OCCURRENCE. Eocene, London Clay ; Whitecliff, Enborne, Studland and Sheppey. *Wetzeliiella (W.) symmetrica* has also been recorded from the Oligocene of Germany (Weiler 1956, Alberti 1961, Gerlach 1961 and Brosius 1963).

Wetzeliiella (Wetzeliiella) symmetrica var. *lobisca* nov.

Pl. 20, fig. 3

1948. *Hystrichosphaeridium articulatum* Pastiels : 43, pl. 4, figs. 13, 17.1961. *Wetzeliiella symmetrica symmetrica* Gerlach : 185, pl. 25, figs. 7, 8.

DERIVATION OF NAME. Latin ; *lobisca*, a small protuberance.

HOLOTYPE. B.M.(N.H.) slide V.51970. London Clay ; Sheppey, Kent, sample 1.

DIMENSIONS. Holotype : outer shell, length 137 μ , breadth 123 μ . Capsule, length 78 μ , breadth 70 μ . Observed range : outer shell, length 125-137 μ , breadth, 118-150 μ . Capsule, length 72-80 μ , breadth 70-79 μ . Number of specimen, measured, 4.

DESCRIPTION. This is a variety of *W. (W.) symmetrica* which has a slightly reduced apical horn and the single antapical horn is offset to the right of the mid-ventral line. It is identical with the two figured specimens of *W. symmetrica symmetrica* Gerlach (1961) and *Hystrichosphaeridium articulatum* Pastiels (1948).

OCCURRENCE. Eocene, London Clay ; Whitecliff, Enborne and Sheppey. It has also been recorded from the Ypresian of Belgium (Pastiels 1948 as *H. articulatum*) and the Oligocene-Miocene of Germany (Gerlach 1961).

Wetzeliiella (Wetzeliiella) varielongituda sp. nov.

Pl. 20, figs. 4, 8

DERIVATION OF NAME. Latin ; *varius*, varied, *longituda*, length.

DIAGNOSIS.Periphragm outline sub-rhomboidal, with short broad lateral horns, a short wide apical horn and one well developed (right) antapical horn. Left

antapical horn represented by slight protuberance on left antapical margin. Capsule thick walled, often coarsely granular. Processes extremely short on ambitus of periphragm and increasing in length further away from ambitus. Distally processes bifid, aculeate, acuminate or evexate.

HOLOTYPE. B.M.(N.H.) slide V.51973. London Clay ; Sheppey, Kent, sample 2.

DIMENSIONS. Holotype : outer shell, length 103μ , breadth 100μ . Capsule, length 73μ , breadth 71μ . Observed range : outer shell, length $96-126\mu$, breadth $90-125\mu$. Capsule, length $64-79\mu$, breadth $63-84\mu$. Length/breadth ratio of pericoel $1-1$ to $1.1-1$. Number of specimens measured, 7.

DESCRIPTION. One of the diagnostic features of *W. varielongituda* are the processes. The wall of the periphragm is up to $1/2\mu$ in thickness, so that the slender processes have only a minute central tubule, along their length. They are distally closed, proximally open to the pericoel. The processes can be granular and are always simple. The shortest processes occur on the ambitus of the pericoel and particularly is this so on the lateral horns and epitract. It is these processes that can be acuminate or evexate distally. The processes are regularly orientated in simulate complexes or are irregular occurring within the complexes. Typical *Wetzelietta* tabulation is decipherable, with the archeopyle intercalary.

The horns of *W. varielongituda* tend to be broad and low, merging imperceptibly with the lateral margins of the periphragm. This is especially so with the apical horn.

The capsule is sub-circular in outline, ellipsoidal in cross section and has a wall up to 3.5μ thick. The wall often shows local thickening directly opposite the horns. Distance of the capsule from the inner surface of the periphragm is variable.

OCCURRENCE. Eocene, London Clay ; Sheppey, Kent.

REMARKS. The nature of the processes, outline of the pericoel and structure of the capsule readily distinguish *Wetzelietta* (*W.*) *varielongituda* from other species of *Wetzelietta*.

Sub-Genus **WETZELIELLA (RHOMBODINIUM)** Gocht 1955

DIAGNOSIS. A sub-genus of the genus *Wetzelietta* that does not possess processes on the periphragm. Tabulation indistinctly shown apart from a transverse cingulum.

TYPE SPECIES. *Wetzelietta* (*Rhombodinium*) *draco* (Gocht 1955). Oligocene ; Germany.

Wetzelietta* (*Rhombodinium*) *glabra Cookson

Pl. 20, figs. 9, 10

1956. *Wetzelietta glabra* Cookson : 186, pl. 2, figs. 1-5.

DISCUSSION. Specimens of *W. glabra* from the London Clay differ from the type material in having only one well developed antapical horn, the right. The left antapical horn is, at the most, represented by a slight protuberance. The transverse

girdle is also less well marked whilst the capsule archaeopyle gives the impression of being apical in some specimens. This may be due to secondary movement of the capsule within the pericoel. The capsule is occasionally found free.

On the outer surface of the periphragm of some individuals are present dendritic ridges, radiating out from central points and being up to 10 or 15 μ across. They are not caused by local thickenings of the wall but by undulations. On an individual there can be a large number of these dendritic radiating structures. They are possibly a result of fungal attack. *W. glabra* is included in the sub-genus *Rhombo-dinium* on account of the absence of processes.

DIMENSIONS. Range observed in London Clay : outer shell, length 140–151 μ , breadth 147–168 μ . Capsule, length 66–80 μ , breadth 69–76 μ . Number of specimens measured, 6.

OCCURRENCE. Eocene, London Clay ; Sheppey, Kent. Eocene ; Australia (Cookson 1956).

X. FURTHER DINOFLAGELLATE CYSTS FROM THE SPEETON CLAY

By W. A. S. SARJEANT

INTRODUCTION

The assemblages of dinoflagellate cysts from the Speeton Clay are both extremely rich and extremely varied. Their description was begun in a previously published paper (Neale & Sarjeant 1962) and a number of species are here dealt with, wherever appropriate, in earlier chapters. All remaining species represented that have been studied to date are described in this chapter, and the stratigraphical distribution of all the constituent species of the assemblages is summarized in tabular form and discussed.

Genus *NETRELYTRON* Sarjeant 1961a : 113

EMENDED DIAGNOSIS. Cavate dinoflagellate cysts, enclosing body spindle-shaped, inner body ovoidal to spindle-shaped. Shell showing no trace of tabulation or of cingulum or sulcus. Shell enclosed in cloak of adherent organic matter, formless or oval to spindle-shaped in outline : fragments of mineral matter and other sedimentary debris sometimes embedded in cloak. Archaeopyle frequently developed : precingular in position.

TYPE SPECIES. *Netrelytron stegastum* Sarjeant 1961a. Upper Jurassic (Oxfordian) ; England.

REMARKS. This genus is characterized by its shape, cavate character and investing mass of organic matter ; formation of a similar debris cloak during encystment is known to occur in some modern dinoflagellates.

The genus *Kalyptea* Cookson & Eisenack 1960b from the Upper Jurassic of Australia, is described as having a " diaphanous veil-like external membrane ", which may correspond to the organic cloak of *Netrelytron* ; the cysts are oval, with one to two horns, but lack an inner body. The somewhat similar genus *Komerwuiia* Cookson & Eisenack 1960b, also from the Upper Jurassic of Australia, lacks either outer cloak or inner body.

Netrelytron trinetron sp. nov.

Pl. 22, fig. 3 ; Text-fig. 51

DERIVATION OF NAME. Greek, *tri-*, three ; *netron*, spindle : referring to the similar shapes of the debris cloak and the enclosing and inner bodies.

DIAGNOSIS. A *Netrelytron* with outer body of basically ovoidal shape, giving rise to strongly tapering, conical apical horn and somewhat shorter, conical antapical horn. Shape of inner body exactly similar. Horns polar and axial in position and direction. Endophragm and periphragm minutely, but densely, granular.

HOLOTYPE. B.M.(N.H.) slide V.51729(1). Speeton Clay, Shell West Heslerton Borehole at 39 metres depth, West Heslerton, Yorks. Lower Cretaceous (Middle Barremian).

DIMENSIONS. Holotype—overall length of enclosing body 90μ , breadth $53\text{--}5\mu$, length of apical horn 18μ , of antapical horn 5μ ; overall length of inner body $67\cdot5\mu$, breadth $38\cdot5\mu$. Range of dimensions; overall length of enclosing body c. $70\text{--}95\mu$.

DESCRIPTION. The holotype is enclosed in a spindle-shaped cloak of debris: in other specimens, the debris cloak appears less well formed.

The outer membrane is spindle-shaped, with unequally developed horns. In the holotype, the apical horn tapers sharply to an acute point from about mid-length: this was not the case in other specimens, where the apical horn tapered more smoothly from base to tip. The inner body is of comparable shape, its apical horn always tapering smoothly from base to tip.

No specimen seen shows a well-developed archaeopyle; however, the holotype shows a slit, corresponding in position to a precingular opening, which may be an archaeopyle that has either incompletely opened or subsequently closed up.



Fig. 51. *Netrellytron trinetrion* sp. nov., showing the shell surrounded by the enclosing cloak of organic matter. $\times$ c. 500.

REMARKS. In the form of the inner body, *Netrelytron trinatron* sp. nov. differs from both other described species of the genus. It has only been recorded to date from one horizon in the West Heslerton Bore, from which some six specimens have been recorded.

OTHER SPECIES

Netrelytron jurassicum (Alberti 1961) from the Middle Jurassic (Bathonian–Callovian) of Germany, is here transferred to this genus from *Kalyptea* on the basis of its possession of an inner body within the spindle-shaped shell.

Brosius (1963 : 38, pl. 3, fig. 2, pl. 4, fig. 2, pl. 5, fig. 4) has described a species from the German Oligocene, as *Netrelytron* sp. nov. This corresponds in most particulars to the emended diagnosis of *Netrelytron*, but lacks a cloak of debris. Erection to separate generic status may prove appropriate.

Genus **PARANETRELYTRON** nov.

DERIVATION OF NAME. Greek, *para*, near ; *netron*, spindle ; *elytron*, sheath, husk—refers to the similarity of this genus to *Netrelytron*.

DIAGNOSIS. Cavate dinoflagellate cysts, enclosing body spheroidal to ovoidal with apical horn ; inner body spheroidal. Shell lacking tabulation, with or without traces of cingulum. Shell enclosed in cloak of adherent matter, formless to oval in outline ; fragments of mineral matter and other sedimentary debris sometimes embedded in cloak. Archaeopyle formation not known.

TYPE SPECIES. *Paranetrellytron strongylum* sp. nov. Lower Cretaceous (Lower Barremian) ; England.

REMARKS. This genus differs from *Netrelytron* in lack of an antapical horn and in presence of indications of a cingulum ; and from all other described genera in the possession of an outer cloak of organic debris.

Paranetrellytron strongylum sp. nov.

Pl. 21, fig. 5 ; Pl. 23, fig. 5 ; Text-fig. 52

DERIVATION OF NAME. Greek, *strongylos*, round, rounded.

DIAGNOSIS. A *Paranetrellytron* having a spheroidal outer body tapering smoothly to form short, blunt apical horn. Inner body spheroidal and relatively large, thin-walled and often hard to distinguish. A poorly-marked cingulum sometimes present. Endophragm and periphragm smooth or only very minutely granular.

HOLOTYPE. B.M.(N.H.) slide 51722(1). Speeton Clay, Shell West Heslerton Borehole at 42.5 metres depth, West Heslerton, Yorks. Lower Cretaceous (Lower Barremian).

DIMENSIONS. Holotype : overall length 56μ , breadth 45μ , length of apical horn 10μ ; length of inner body $c.40\mu$, breadth $c.40\mu$. Range of dimensions : overall lengths $51-58\mu$.

DESCRIPTION. The holotype is enclosed in a roughly oval cloak of debris ; in the three other specimens observed to date, the debris cloak was comparable. The enclosing body is roughly lemon-shaped. The inner body fits quite closely, except at the apical end where there is a quite large expansion of the pericoel. It is thin and transparent and, as a result, very hard to distinguish ; its presence was confirmed only under phase contrast.

The debris cloak of the holotype contains a ball-like mass of debris immediately posterior to the antapex. This structure is of doubtful significance and may simply represent fortuitous adherence of organic debris from a quite unrelated source. An archaeopyle has not been observed to date.

REMARKS. *Paranetrelytron strongylum* sp. nov. occurs in the 39 and 42.5 metres horizons in the West Heselton Borehole (Lower to Middle Barremian). Its small size and debris cloak render it especially inconspicuous ; further studies may well indicate a much wider distribution.

Genus **MUDERONGIA** Cookson & Eisenack 1958 : 40

TYPE SPECIES. *M. mcwhaei* Cookson & Eisenack 1958. Lower Cretaceous (Aptian) ; Australia.

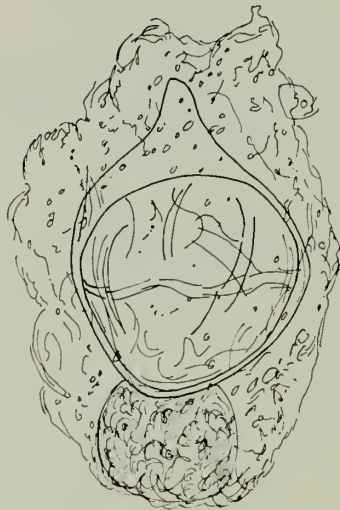


FIG. 52. *Paranetrelytron strongylum* sp. nov., showing the shell surrounded by the enclosing cloak of organic matter. $\times c. 750$.

Muderongia staurota sp. nov.

Pl. 21, figs. 6, 7 ; Pl. 23, fig. 4 ; Text-fig. 53

DERIVATION OF NAME. Greek, *staurotos*, cruciform.

DIAGNOSIS. A *Muderongia* having an ovoidal to ellipsoidal enclosing body, prolonged into four strong horns. Apical horn strong and tapering, length slightly less than length of shell alone. Lateral horns quite short, less than shell breadth, at first almost parallel sided, but at about one-third length, anterior margin tapering backward to form an angle with posterior margin. Antapical horn basically conical, with slight out-bulge at one side ; length also less than length of shell alone. Inner body ovoidal to ellipsoidal. Periphragm smooth or finely pitted ; endophragm varying from smooth to densely granular. Shell showing neither trace of tabulation nor of cingulum or sulcus. An apical archaeopyle is formed.

HOLOTYPE. B.M.(N.H.) slide V.51724(3). Speeton Clay, Shell West Heslerton Borehole at 42.50 metres depth, West Heslerton, Yorkshire. Lower Cretaceous (Lower Barremian).

PARATYPE. B.M.(N.H.) slide V.51718(3). Same locality and horizon.

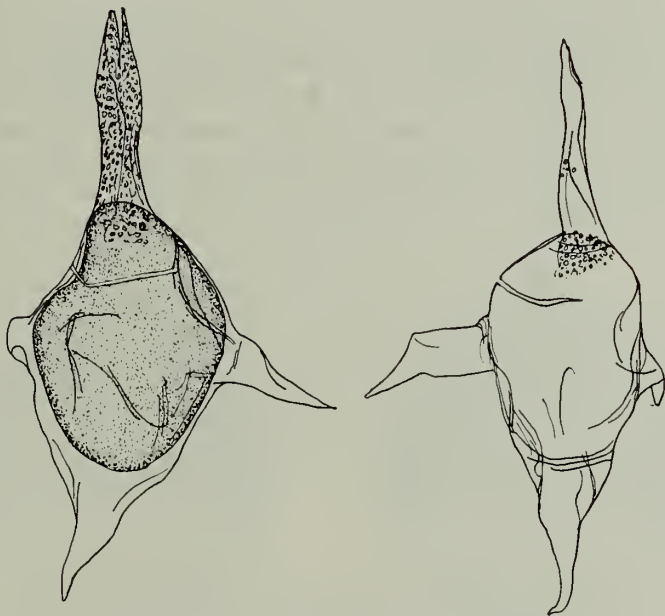


FIG. 53. *Muderongia staurota* sp. nov. Left, holotype. Right, paratype. The variation in proportions and in degree of granularity of the inner body is shown : the holotype shows incipient formation of an archaeopyle. $\times$ c. 500.

DIMENSIONS. Holotype—overall length 170μ , breadth 93μ ; length of apical horn (tip missing) 55μ , of antapical horn 34.5μ , of longer lateral horns 26μ , length of inner body, 70μ , breadth 55μ . Paratype—overall length 145μ , breadth 80μ ; length of apical horn, 47μ , of antapical horn, $c.44\mu$, of longer lateral horns $c.31\mu$; length of inner body $c.56\mu$, breadth $c.51\mu$. These two specimens represent opposite extremes of the observed range of variation.

DESCRIPTION. The enclosing body has a basically cruciform outline, with a distinctly oval shell enclosing, more or less tightly, an inner body of similar shape. The lateral horns show no distinct notch, nor is a second, shorter antapical horn developed; however, the backward curve of the lateral horns and the lateral bump on the antapical horn suggest affinity to species showing these features.

The periphragm shows some degree of pitting, variable in degree and location but usually especially dense on the apical horn. The inner body varies from smooth to granular; where it is smooth, the inner body becomes hard to distinguish and may only be confirmed under phase contrast. (The holotype and paratype illustrate this variation.)

This species is relatively common in the Lower Barremian of the West Heselton Borehole: over 20 specimens were noted, of which the majority comprised either detached apices or shells lacking an apex, complete shells being relatively infrequent. Both holotype and paratype show incipient development of an archaeopyle.

REMARKS. *Muderongia staurota* sp. nov. is characterized by the morphology of its shell processes. In contrast *M. mcwhaei* has a pronouncedly rhombic shell outline; proportionately longer and slimmer horns; notched lateral horns and a second, short antapical horn. *M. simplex* Alberti 1961, from the Lower Cretaceous (Hauterivian to Valanginian) of Germany and Bulgaria, has short horns of almost equivalent relative length, the lateral horns being blunt and notched, and a second antapical horn being again developed. *M. perforata* Alberti 1961, from the Upper Cretaceous (Turonian) of Germany, has very strong, thick horns, the second antapical horn being especially pronounced. *M. tetracantha* (Gocht 1957), from the Lower Cretaceous (Hauterivian) of Germany, has in contrast extremely long and delicate horns; a second antapical horn is lacking, but the notching of the lateral horns is so deep as to approach bifurcation into unequal branches. *M. tomaszowensis* Alberti 1961, from the Lower Cretaceous (Valanginian) of Germany and Poland, has stubby apical and antapical horns and blunt notched lateral horns. *M. crucis* Neale & Sarjeant 1962, from the Lower Cretaceous (Hauterivian) of England, is extremely large (overall length $250-325\mu$), with long axial horns and long lateral horns, the latter backswept and not notched.

Genus *APTEODINIUM* Eisenack 1958c

TYPE SPECIES. *A. granulatum* Eisenack 1958c. Lower Cretaceous (Aptian); Germany.

Apteodinium maculatum Eisenack & Cookson

Pl. 22, fig. 1 ; Text-fig. 54

1960. *Apteodinium maculatum* Cookson & Eisenack : 4, pl. 2, figs. 1-3.

REMARKS. This species, hitherto recorded only from the Lower Cretaceous (Aptian to Albian) of Australia, occurs in low numbers in the assemblages from the Shell West Heselton Borehole, West Heselton, Yorkshire, at 42.50 metres depth. (Lower Barremian).

The English specimens are somewhat smaller than the Australian type material : the figured specimen (B.M.(N.H.) slide V.51718(4)), with overall length 75μ , breadth 64μ , falls a little below the quoted Australian range of length $74-105\mu$, breadth $70-105\mu$. There are faint indications of a sulcus and the "small thickened areas with circular outlines" noted by Eisenack and Cookson are totally lacking. Nor has an archaeopyle been observed to date. (The "hoof-shaped pylome" mentioned by those authors must be interpreted as a precingular archaeopyle.) However, the triviality of these differences and the complete correspondence in other characters does not justify any nomenclatural distinction of the English specimens, which accordingly represent a considerable extension in the geographic and stratigraphic range of this species.

Genus *DOIDYX* nov.

DERIVATION OF NAME. Greek, *doidyx*, pestle, in reference to the shell shape.

DIAGNOSIS. Proximate dinoflagellate cysts with flattened biconical shell, pronouncedly asymmetrical. Epitract in form of high cone which may be drawn out into an apical horn, giving a mammillate appearance : hypotract in form of flattened cone, with or without antapical prominence. Shell bulging out laterally to one side more than to the other ; lateral horns lacking. Greater part of shell surface covered

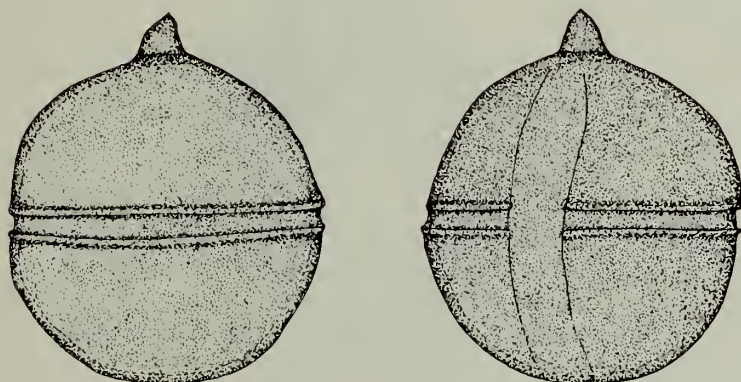


FIG. 54. *Apteodinium maculatum* Eisenack & Cookson, showing the dense granulosity and the positions of cingulum and sulcus. $\times$ c. 800.

with short spines, simple or bifurcate : arrangement is in general random, but sometimes in rows, suggesting traces of tabulation. Equatorial zone, corresponding to cingulum, lacking spines : not hollowed. No pattern of sutures visible, no clear indication of sulcus. Apical archaeopyle formed by schism of shell on angular line of breakage.

TYPE SPECIES. *Doidyx anaphrissa* sp. nov. Lower Cretaceous (Lower Barremian) ; England.

REMARKS. In its asymmetrically biconical shell, spine cover and absence of tabulation, this new genus differs from all described fossil genera. The asymmetry and mode of archaeopyle formation suggests a probable derivation from the genus *Pseudoceratium* by reduction of polar horns and loss of the lateral horn.

Doidyx differs from *Diconodinium*, *Palaeohystrichophora* and *Dioxya* in its asymmetrical shape : from *Diconodinium* also in the absence of a sulcus : from *Palaeohystrichophora* also in the lack of an inner body ; and from *Dioxya* in the clear indication of a cingulum. It differs from the superficially similar genus *Aptea* in the lack of an enclosing membrane.

Doidyx anaphrissa sp. nov.

Pl. 22, fig. 8 ; Pl. 23, fig. 6 ; Text-fig. 55

DERIVATION OF NAME. Greek, *anaphrisso*, to bristle.

DIAGNOSIS. A *Doidyx* having an asymmetrically biconical shell with short, blunt apical horn and with low bump on antapex. Spines simple, capitate or briefly bifurcate. Portion thrown off in archaeopyle formation exceeding one-third of shell length.

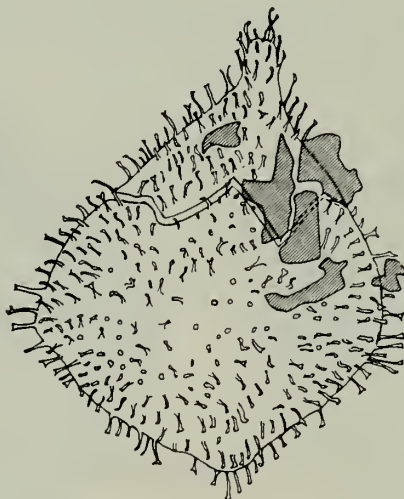


FIG. 55. *Doidyx anaphrissa* sp. nov. Holotype, showing archaeopyle formation. $\times$ c. 750.

HOLOTYPE. B.M.(N.H.) slide V.51723(3). Speeton Clay, Shell West Heslerton Borehole, West Heslerton, Yorks., at 42.5 metres depth. Lower Cretaceous (Lower Barremian).

DIMENSIONS. Holotype—overall length 105μ , breadth 118μ ; shell length 11μ , breadth 102μ ; spines c. 7μ long. Range of dimensions: overall lengths c. 120 – 145μ , breadths c. 105 – 130μ .

DESCRIPTION. This species is moderately abundant, some 25 specimens having been encountered; complete shells were infrequent, detached apices and shells lacking an apex being commoner.

The shell is approximately club-shaped: its asymmetry is so pronounced that a longitudinal division would leave some 60% on one side, some 40% on the other. The epitract slopes smoothly into the apical horn; the hypotract is surmounted by an antapical bulge of small height and larger amplitude. The surface is very minutely granular.

There is a dense cover of short spines, most often capitate, less frequently evexate, oblate, bifid or bifurcate: these sometimes suggest arrangement into lines, but no coherent pattern was determined. An equatorial belt of moderate breadth, corresponding to the cingulum, lacks spines: a sulcus is not distinguishable.

The holotype shows fission to form an archaeopyle, which has however, not become detached. Its margin is distinctly angular, suggesting a tabulation pattern not otherwise indicated.

REMARKS. In its combination of shape, process cover and mode of archaeopyle formation, *Doidyx anaphrissa* sp. nov. differs from all other described species.

Genus **BROOMEA** Cookson & Eisenack 1958: 41

TYPE SPECIES. *B. ramosa* Cookson & Eisenack 1958. Middle–Upper Jurassic; Australia.

?*Broomea longicornuta* Alberti

Pl. 21, fig. 1

1961. ?*Broomea longicornuta* Alberti: 27, pl. 5, figs. 18–21, pl. 6, figs. 1, 2.

REMARKS. This species, originally described from the Lower Cretaceous (Hauterivian–Upper Barremian) of Germany, is represented by a single specimen in the assemblage from the Speeton Clay of the West Heslerton Borehole at 19.25 metres depth (Upper Barremian). The dimensions of this specimen, B.M.(N.H.) slide V.51733(1), are overall length c. 285μ ; shell length 100μ , breadth 48μ ; length of apical horn c. 130μ ; length of unbent antapical horn 55μ . This falls within the range of overall lengths quoted by Alberti (248–298 μ).

Genus **ODONTOCHITINA** Deflandre 1935a : 234

TYPE SPECIES. *Ceratium* (*Euceratium*) *operculatum* O. Wetzel 1933. Upper Cretaceous ; Germany.

Odontochitina operculata (O. Wetzel)

Pl. 21, fig. 2

- 1933. *Ceratium* (*Euceratium*) *operculatum* O. Wetzel : 170, pl. 11, figs. 21–22.
- 1935. *Odontochitina silicorum* Deflandre : 234, pl. 10, figs. 8–10.
- 1937. *Odontochitina silicorum* Deflandre ; Deflandre : 47, pl. 18, figs. 8–10.
- 1946. *Odontochitina operculata* (O. Wetzel) Deflandre, cards 1016–19.
- 1948. *Palaeoceratium operculatum* (O. Wetzel) O. Wetzel : ?342.
- 1950. Dreihörnige Hüllen mit Stachelkleid, O. Wetzel : 170, pl. 13, fig. 6.
- 1952. *Odontochitina operculatum* (O. Wetzel) ; Firtion : 160, pl. 8, fig. 9.
- 1955. *Odontochitina operculata* (O. Wetzel) ; Deflandre & Cookson : 291, pl. 3, figs. 5, 6.
- 1955. *Odontochitina operculata* (O. Wetzel) ; Deflandre-Rigaud : 19.
- 1955. *Odontochitina operculata* (O. Wetzel) ; Valensi : 594, pl. 4, fig. 7.
- 1958. *Odontochitina operculata* (O. Wetzel) ; Eisenack : 393, pl. 27, figs. 7, 8.
- 1959. *Odontochitina operculata* (O. Wetzel) ; Gocht : 64, pl. 6, fig. 12.
- 1961. *Odontochitina operculata* (O. Wetzel) ; Alberti : 30, pl. 6, figs. 6–9.
- 1961. *Odontochitina operculata* (O. Wetzel) ; Eisenack : 323, pl. 36, fig. 3.
- 1962. *Odontochitina silicorum* Deflandre ; Pocock : 78, pl. 14, figs. 211, 212.
- 1963. *Odontochitina operculata* (O. Wetzel) ; Górka : 35, pl. 4, figs. 1–5.
- 1963. *Odontochitina operculata* (O. Wetzel) ; Balteş : 584, pl. 5, figs. 1–4.
- 1964. *Odontochitina operculato* (O. Wetzel) ; Singh : 147, pl. 20, figs. 9, 10.

REMARKS. This species is long-ranging and widespread : it has been recorded from the Upper Jurassic of Canada by Pocock (1962) and has a well-documented range in the Cretaceous, from Upper Hauterivian to Campanian. It is present in low numbers in the assemblages from 19–25 metres depth in the Shell West Heslerton Borehole (Upper Barremian). All specimens seen lacked the apex ; the figured specimen, B.M.(N.H.) slide V.51730(4), is the best-preserved, having an overall length of 133·5 μ , breadth 88 μ , the central body being 53 μ long and 48 μ broad, the lateral horn c.55 μ long and the antapical horn 83·5 μ long. The range in dimensions observed was overall lengths 120–133·5 μ , breadths 67–100 μ : these fall well within the previously quoted ranges. Detached horns, probably of *O. operculata*, were also observed.

Odontochitina operculata is also present at all levels in the Cenomanian of the H.M. Geological Survey Borehole at Fetcham Mill, Surrey.

Genus **FROMEA** Cookson & Eisenack 1958 : 55

TYPE SPECIES. *Fromea amphora* Cookson & Eisenack 1958. Cretaceous (Aptian to Cenomanian) ; Australia.

Fromea amphora Cookson & Eisenack

Pl. 22, fig. 4 ; Pl. 23, fig. 3

1958. *Fromea amphora* Cookson & Eisenack : 56, pl. 5, figs. 10, 11.1961. *Fromea amphora* Cookson & Eisenack ; Alberti : 23, pl. 12, fig. 13.?1961. Chrysomonadiniae? Maliavkina *et al.*, pl. 52, figs. 1-5.

REMARKS. This species, originally described from somewhat higher horizons in Australia, has been recorded by Alberti from the Upper Barremian of Germany and occurs at this level in the Shell West Heselton Borehole (at 19.25 metres depth). The figured specimens, B.M.(N.H.) slide V.51732(1, 2), are of closely similar size, respectively measuring $84 \times 49\mu$ and $84 \times 50\mu$, the apex being lacking ; this is within the range quoted for the Australian specimens ($62-95\mu \times 47-81\mu$) and larger than that quoted for the German specimens ($58-66\mu \times 49-52\mu$).

The shell surface is minutely granular in these specimens ; there is little indication of a cingulum.

The specimens figured by Maliavkina *et al.* (1961, pl. 52, figs. 1-5), from the Maestrichtian of Siberia, may be examples of *Fromea amphora*, but are rather small.

Genus *SYSTEMATOPHORA* Klement 1960 : 61

TYPE SPECIES. *S. areolata* Klement 1960. Upper Jurassic (Kimmeridgian) ; Germany.

Systematophora schindewolfi (Alberti)

Pl. 22, fig. 5

1961. *Hystriosphærina schindewolfi* Alberti : 38, pl. 10, figs. 1-3, 6, 7.1962. *Systematophora schindewolfi* (Alberti) Neale & Sarjeant : 455 (by implication).

REMARKS. This species, originally described from the Cretaceous (Upper Barremian to ?Senonian) of Germany, has been encountered only in the horizon from 42.5 metres depth in the Shell West Heselton Borehole (Middle Barremian). The majority of examples are too obscured or badly positioned for study, but one specimen, B.M.(N.H.) slide V.517121(1), was excellently preserved and favourably orientated. Its dimensions (overall length 120μ , breadth 112μ ; shell length 65μ , breadth 60μ) accord with those quoted by Alberti (shell length $58-70\mu$; length of appendages $22-39\mu$).

Study showed that the distribution of the annular process complexes on epittract and hypottract, and the linear equatorial complexes, was precisely that specified for the genus by Klement.

Genus *GARDODINIUM* Alberti 1961 : 18

TYPE SPECIES. *Gardodinium eisenacki* Alberti 1961. Lower Cretaceous (L. Hauterivian to Aptian) ; Germany.

Gardodinium eisenacki Alberti

Pl. 21, fig. 4

1961. *Gardodinium eisenacki* Alberti : 18, pl. 3, figs. 8-13.

REMARKS. This species occurs in moderate abundance in the assemblages from 39 metres and 42.5 metres depth. Specimens are frequently distorted. The figured specimen, B.M.(N.H.) slide V.51726(1), is the best preserved ; its dimensions are overall length 76μ , breadth 55μ ; shell length 56μ , breadth 50μ . The range of dimensions exhibited accords closely with that quoted by Alberti ($77-85\mu \times 55-60\mu$ overall).

Genus *DINGODINIUM* Cookson & Eisenack 1958 : 39

TYPE SPECIES. *Dingodinium jurassicum* Cookson & Eisenack 1958. Upper Jurassic ; Papua and Australia.

?Dingodinium albertii sp. nov.

Pl. 21, fig. 3, Pl. 23, fig. 1

1961. *Dingodinium* sp. A., Alberti : 17, pl. 3, fig. 16.

DERIVATION OF NAME. Named in honour of Dr. Gerhard Alberti, the first to describe this form of cyst.

DIAGNOSIS. A cavate dinoflagellate cyst with thin outer shell, irregularly ovoidal to subpolygonal in outline, drawn out into a blunt, stout apical horn ; inner body thin, spheroidal, with dense cover of large, pointed tubercles. Outer shell possessing clear helicoid cingulum marked by prominent folds or ridges ; further folds or ridges, less prominent, define tabulation. Intercalary archaeopyle apparently formed.

HOLOTYPE. B.M.(N.H.) slide V.51719(2). Speeton Clay, Shell West Heslerton boring at 42.50 metres depth, West Heslerton, Yorks. Lower Cretaceous (Lower Barremian).

PARATYPE. B.M.(N.H.) slide V.51723(1). Same locality and horizon.

DIMENSIONS. Holotype—overall length 66μ , breadth 52μ , length of inner body 40μ , breadth 45μ . Paratype—overall length 57μ , breadth 48μ , length of inner body 37μ , breadth 39μ . Range of dimensions—overall lengths $50-66\mu$, breadths $37.5-52\mu$.

DESCRIPTION. The outer shell is basically ovoidal to polygonal ; but it is extremely thin and is deformed in variable fashion in the seven specimens examined. It bears folds or ridges which simulate a tabulation and is drawn out into a short apical horn with a blunt, slightly rounded tip. The inner body is spheroidal and typically broader than long. The periphragm is smooth ; the endophragm smooth or very minutely granular. The latter bears a moderately dense cover of tubercles ; these are conical and do not exceed 1μ in height. There is some suggestion that the tubercles show a degree of alignment, but this could not be confirmed.

The archaeopyle is situated on the upper flanks of the epitract, in a position corresponding to the intercalary archaeopyle described by Evitt (1961c, text-fig. 7). The tabulation pattern was not sufficiently clear, however, to permit certainty as to whether the archaeopyle corresponded in position to an intercalary plate; it is equally possible to visualize formation by loss of the equivalent of the anterior part only of a precingular plate.

REMARKS. Alberti (1961) recorded this form from the Lower Cretaceous (Upper Barremian) of Germany and commented that it probably constituted a new species. It occurs in the Lower Barremian horizons of the Speeton Clay (at 39 metres and 42.5 metres depth), but has not to date been encountered in the Upper Barremian.

The generic allocation is made, following Alberti, on the basis of the tuberculate structure of the inner body; however, a tabulation is typically absent in *Dingodinium*. It was not possible to determine the plate pattern in detail, but there proved to be some similarity to the pattern exhibited in *Scriniodinium* subgenus *Endoscrinium* Klement 1960c, to which the species is thus possibly referable.

In the relative shapes of outer shell and inner body and in the ornamentation of the inner body? *Dingodinium albertii* sp. nov. differs from all other described species.

Genus *PAREODINIA* Deflandre 1947 : 4

TYPE SPECIES. *Pareodinia ceratophora* Deflandre 1947. Middle Jurassic; France.

Pareodinia ceratophora Deflandre

Pl. 23, fig. 2

- 1947. *Pareodinia ceratophora* Deflandre : 4, text-figs. 1-3.
- 1958. *Pareodinia aphelia* (para) Cookson & Eisenack : 60, pl. 12, fig. 9.
- 1958. *Cryptomeriapollenites coralliensis* Lantz (nom. nud.) : 927, pl. 5, figs. 55-56, pl. 6, fig. 7.
- 1958. Incertae sedis, Lantz : 927, pl. 6, figs. 58-59.
- 1960b. *Pareodinia ceratophora* Deflandre ; Sarjeant, pl. 12, fig. 11.
- 1961a. *Pareodinia ceratophora* Deflandre ; Sarjeant : 99, pl. 13, fig. 16.
- 1961. *Pareodinia ceratophora* Deflandre ; Alberti : 23, pl. 12, fig. 14.
- 1961. Peridinea (?) Maliavkina, Samoilovitch *et al.*, pl. 16, figs. 1, ?2.
- 1961. *Pareodinia* sp., Evitt, pl. 8, fig. 19.
- 1962a. *Pareodinia ceratophora* Deflandre ; Sarjeant : 263, pl. 1, fig. 13.
- 1962b. *Pareodinia certophora* Deflandre ; Sarjeant : 483, pl. 69, fig. 8 ; text-fig. 5.
- 1963. *Pareodinia ceratophora* Deflandre ; Baltes : 584, pl. 4, fig. 7 (mis-spelt *P. cerathophora* in text).

REMARKS. This species, first described from the Middle Jurassic, is known to occur also in the Upper Jurassic. Cookson & Eisenack (1958) embraced within their species *Pareodinia aphelia*, from the Upper Jurassic to Lower Cretaceous of Australia, what they recognized as two distinct morphological entities; one of these (type 2) corresponds exactly with *Pareodinia ceratophora*. In the Speeton Clay, this species is represented by a handful of specimens in the Hauterivian and Barremian horizons; in the absence of any other evidence of reworking these must be presumed to be

indigenous. *P. ceratophora* thus emerges as having a known range from Callovian to Barremian. The shape and dimensions of the Speeton specimens accord with the range quoted by Deflandre as typical (overall length 65–78 μ), the figured specimen, B.M.(N.H.) slide V.51724(4), having an overall length of 71 μ , with apical horn 13.5 μ long, and a breadth of 57.5 μ .

Genus *SIRMIODINIUM* Alberti 1961 : 22

TYPE SPECIES. *S. grossi* Alberti 1961. Lower Cretaceous (U. Hauterivian–U. Barremian) ; Germany.

Sirmiodinium grossi Alberti

Pl. 22, fig. 7

1961. *Sirmiodinium grossi* Alberti : 22, pl. 7, figs. 5–7, pl. 12, fig. 5.

REMARKS. This species is represented in four studied horizons of the Speeton Clay, at 39.0, 42.5, 99.25 and 103.25 metres depth. (Middle Hauterivian to Lower Barremian.) The range of dimensions exhibited is similar to, but somewhat greater than, that quoted by Alberti (overall length 87–92 μ , breadth 81–85 μ) ; the figured specimen, B.M.(N.H.) slide V.51722(2), having the dimensions overall length 95 μ , breadth 85 μ , length of inner body 65 μ , breadth 63 μ .

Genus *COMETODINIUM* Deflandre & Courteville 1939 : 98

TYPE SPECIES. *C. obscurum* Deflandre & Courteville 1939. U. Cretaceous ; France.

Cometodinium sp.

Pl. 22, fig. 6

DESCRIPTION. Shell spherical to spheroidal, minutely granular, densely covered by a mat of undulose hairlike spines. The spine-cover is lacking only in a narrow median belt corresponding to the cingulum ; this may be partly or wholly obscured from view, by the tangled spines. Archaeopyle not seen.

FIGURED SPECIMEN. B.M.(N.H.) slide V.51723(2), Speeton Clay, Shell West Heselton Borehole at 42.5 metres depth, West Heselton, Yorks. Lower Cretaceous (Lower Barremian).

DIMENSIONS. Figured specimen : overall length 62 μ , breadth 68 μ , shell length 37 μ , breadth 44 μ , length of spines around 15 μ . Dimensions of other specimens closely similar.

REMARKS. This form has been encountered only at one horizon, in low numbers. It differs from *Cometodinium obscurum* in the lack of ridges edging the furrow ; the absence of any indication of a sulcus ; and the considerably shorter spines. It is perhaps more closely comparable to *Baltisphaeridium whitei* (Deflandre & Courteville 1939), also from the Cretaceous of France ; this latter species lacks any trace of a

cingulum, but then the cingulum is by no means easily seen in the Speeton specimens. It is therefore considered better not to propose a new name for these forms.

Genus **WETZELIELLA** Eisenack 1938c : 186

?*Wetzelietta neocomica* Gocht

1957. ?*Wetzelietta neocomica* Gocht ; 172, pl. 19, figs. 1-4, pl. 20, figs. 4, 6, 7 ; text-figs. 7, 8, 15, 16.

1961. ?*Wetzelietta neocomica* Gocht ; Alberti : 11, pl. 4, figs. 17-19.

REMARKS. This species is represented by a number of poorly preserved specimens from two horizons (Hauterivian, 99.25 and 103.25 metres depth) of the Speeton Clay ; their dimensions fall within the range quoted by Gocht (overall length 72-117 μ , breadth 50-94 μ) but only one specimen (B.M.(N.H.) slide V.51715(1)) is sufficiently well displayed to be measured in detail (overall length 103 μ , breadth 90 μ). The attribution of this species to the genus *Wetzelietta* was made with hesitation by Gocht and must be considered doubtful, since archaeopyle formation is apical and not intercalary as in typical species of that genus. However, the English specimens are too poorly preserved to be used as bases for the erection of a new genus.

It is probable that this species is related to *Muderongia*. Evitt (1961 : 397, pl. 8, figs. 1, 2) has figured as " Form G " a species from the Lower Cretaceous Dilkuna Formation of Pakistan which appears exactly intermediate between this latter genus and ?*W. neocomica*.

?*Wetzelietta neocomica* was originally recorded from the Middle Hauterivian of Germany (Gocht 1957). Alberti (1961) has recorded it from the Lower Hauterivian to Upper Barremian of Germany, from the Hauterivian of Poland and Bulgaria and from the Upper Cretaceous (Turonian and Coniacian) of Germany. The fact that it has not yet been recorded from the Aptian, Albian or Cenomanian suggests that the Upper Cretaceous specimens were reworked.

CONCLUSIONS

The known distribution of species of fossil dinoflagellate cysts in the five Speeton Clay horizons examined, is shown in the accompanying Table. A striking feature which emerges is the major change occurring in the Upper Barremian, when the incoming of seven species combines with the disappearance of seven others to change the whole character of the assemblage. The apparent change between the assemblages from 99.25 metres depth (basal Upper Hauterivian) and 42.5 metres depth (upper Lower Barremian) may be expected to fade out when intermediate assemblages are examined.

The 41 species listed in the table do not constitute the full array of dinoflagellate cysts from these five horizons ; there remains a number of species present in low numbers only and hitherto represented by damaged or obscured specimens, not capable of full description. The Speeton assemblages as a whole are remarkably rich and varied : it is clear that a number of species having a relatively limited stratigraphic range will prove of considerable value as stratigraphic indices.

TABLE 5

Horizon in the Speeton Clay of Shell West Heslerton No. 1 bore- hole, West Heslerton, Yorks.	103.25 metres depth (Middle Hauterivian)	99.25 metres depth (Upper Hauterivian)	42.5 metres depth (Lower Barremian)	39.0 metres depth (Middle Barremian)	19.25 metres depth (Upper Barremian)
Species					
<i>Gonyaulacysta cretacea</i>	x	x			
<i>G. palla</i>			x		
<i>G. helicoidea</i>			x	x	
<i>G. axicerastes</i>				x	
<i>G. orthoceras</i>					
<i>G. episoma</i>					x
<i>G. hadra</i>					x
<i>G. aichmetes</i>					x
<i>Heslertonia heslertonensis</i>	x	x	x	x	x
<i>Heliodinium patriciae</i>	x	x			
<i>Hystrichodinium ramoides</i>		x			
<i>Cribroperidinium sepimentum</i>	x	x			
<i>Leptodinium alectrolophum</i>				x	
<i>Pareodinia ceratophora</i>		x	x	x	x
<i>Pseudoceratium</i> (<i>Eopseudoceratium</i>) <i>gochti</i>		x	x	x	
<i>Gardodinium eisenacki</i>	x	x	x		
<i>G. albertii</i>	x	x			
<i>Muderongia crucis</i>		x			
<i>M. staurota</i>			x		
? <i>Wetzeliella neocomica</i>	x	x			
<i>Odontochitina operculata</i>					x
? <i>Broomea longicornuta</i>					x
<i>Doidyx anaphrissa</i>			x		
<i>Apteodinium maculatum</i>			x		
<i>Dingodinium albertii</i>			x		
<i>Netrelytron trinetron</i>				x	
<i>Paranetrelytron strongylum</i>			x	x	
<i>Sirmiodinium grossi</i>	x	x	x	x	
<i>Cometodinium</i> sp.			x		
<i>Fromea amphora</i>					x
<i>Systematophora complicata</i>		x	x	x	
<i>S. schindewolfi</i>			x		
<i>Hystrichosphaera ramosa</i> v. <i>ramosa</i>				x	x
<i>H. ramosa multibreva</i>	x	x	x	x	x
<i>Hystrichosphaeridium simplicispinum</i>		x	x	x	x
<i>H. arborispinum</i>			x	x	
<i>Oligosphaeridium complex</i>		x	x	x	x
<i>O. vasiformum</i>	x	x	x		
<i>O. macrotubulum</i>	x	x			
? <i>Cordosphaeridium fasciatum</i>			x		
<i>Callaiosphaeridium asymmetricum</i>	x	x	x	x	x

Stratigraphical distribution of dinoflagellate cysts in the Speeton Clay of Shell West Heslerton No. 1 Bore.

XI. FURTHER DINOFLAGELLATE CYSTS FROM THE LONDON CLAY

By G. L. WILLIAMS & C. DOWNIE

INTRODUCTION

A number of species of dinoflagellate cysts from the London Clay have been discussed in earlier chapters. However, there remains a large residue of species also considered to be indigenous ; these are discussed in the ensuing pages. Further work on assemblages from the lower part of the London Clay of the Sheppey area and from the Thanet Sands (horizons considered to be Paleocene) is at present in progress at Sheffield by Mr. A. Husain.

Genus *ADNATOSPHAERIDIUM* nov.

DIAGNOSIS. Chorate cysts bearing tubular or solid intratabular processes varying in number on a single plate. Processes united distally by interconnecting trabeculae. Archaeopyle apical.

TYPE SPECIES. *Adnatosphaeridium vittatum* sp. nov.

DISCUSSION. Evitt (1961c) suggested that, in a taxonomic subdivision of *Cannosphaeropsis* into separate genera, three factors needed to be taken into consideration : the type of archaeopyle ; the structure of the processes ; and the nature of the interconnections between processes. All these points need consideration, but the information at present available permits a subdivision into only two genera, recognized by type of archaeopyle and the position of processes with regard to plates. It is acknowledged that species now placed within *Adnatosphaeridium* represent different morphological types and that further subdivision will be necessary. *Adnatosphaeridium* includes species formerly placed in *Cannosphaeropsis*, which on account of their intratabular processes, apical archaeopyle and spherical to ellipsoidal shape, must be placed in a separate taxonomic category. When an archaeopyle is present, species of *Adnatosphaeridium* can be readily distinguished from those of *Cannosphaeropsis*.

Adnatosphaeridium vittatum sp. nov.

Pl. 24, figs. 3, 7 ; Text-fig. 56

DERIVATION OF NAME. Latin ; *vittatus*, decorated or bound with ribbons.

DIAGNOSIS. Ellipsoidal central body, with thin granular wall bearing processes of two types : slender to broadly taeniate, greatly expanded distally, and hollow open branched. Former type predominating. Adjacent processes often united distally. Reflected tabulation ?', 6'', 5''', 1p and 1'''''. Archaeopyle apical.

HOLOTYPE. B.M.(N.H.) slide V.519176(1). London Clay ; Sheppey, Kent, sample Sh.3.

DIMENSIONS. Holotype : diameter of central body 37 μ , by 47 μ , length of processes up to 20 μ . Observed range : diameter of central body, width 37–66 μ ,

length 28 (when archaeopyle present) to 52μ ; Length of processes up to 31μ . Number of specimens measured, 4.

DESCRIPTION. *Adnatosphaeridium vittatum* has strongly developed taeniate processes, often exceeding 10μ in width, which may be arranged in linear, soleate, or annular complexes. In outline, the complexes can be tubiform to flaring, distally having two orthogonal or recurved branches. The outer margin of the branches is frequently finely serrate. Branches of processes are interconnected with other processes on the same or adjacent plates. The interlinking of processes gives to them the appearance of natural arches. Some of the processes are simple and are oblate or bifid distally. Occasionally hollow branched open processes are present on the central body. Unconnected acuminate spines may arise from the processes.

OCCURRENCE. Eocene, London Clay ; Sheppey, Kent.

REMARKS. *A. vittatum* is characterized by its taeniate processes of varying width, the presence of free and united processes and the occasional hollow branched processes. The distal serrate terminations are unusual in this genus.

***Adnatosphaeridium multispinosum* sp. nov.**

Pl. 24, fig. 5 ; Text-fig. 57

DERIVATION OF NAME. Latin ; *multus*, much, many ; *spinosus*, thorny.

DIAGNOSIS. Ellipsoidal central body with thin granular endophragm. Archaeopyle apical, with zigzag margin. Periphragm forming numerous processes, slender, branched distally. Trabeculae possessing single unconnected acuminate spines.

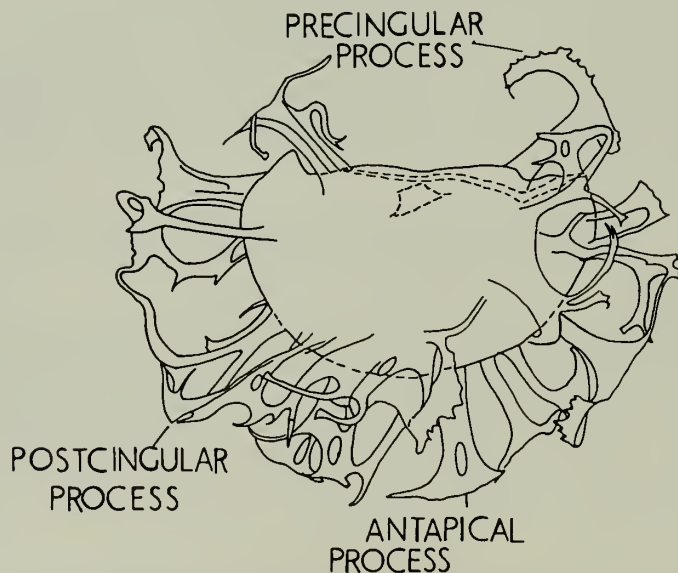


FIG. 56. *Adnatosphaeridium vittatum* sp. nov.

HOLOTYPE. B.M.(N.H.) slide V.51975(1). London Clay ; Whitecliff, sample WC 16.

DIMENSIONS. Holotype : diameter of central body 44 by 59 μ . Length of processes up to 23 μ . Observed range : diameter of central body 44–71 μ . Length of processes up to 23 μ . Number of specimens measured, 3.

DESCRIPTION. The processes of *A. multispinosum* are of approximately equal length in an individual and rarely exceed half the smaller diameter of the central body. They are erect or slightly curved, taeniate, branching from two thirds along their length to the distal extremity. The trabeculae often have short unconnected spines, sometimes arising from bulbous swellings ; the spines can be slender, up to 6 μ in length or short and conical. Occasional wider processes occur. The arrangement of the processes on the central body is variable ; they can lack any regularity or be in soleate or annular complexes.

OCCURRENCE. Eocene, London Clay ; Whitecliff.

REMARKS. *A. multispinosum* differs from *A. filiferum* (= *Cannosphaeropsis filifera* Cookson & Eisenack) in possessing more numerous, generally very slender processes which can branch from two thirds along their length. *Cannosphaeropsis tutulosa* Cookson & Eisenack (1960a), from the Upper Cretaceous of Australia, has fewer processes which divide distally and join with neighbouring branches to form a series of relatively wide deep loops apparently lacking spines.

?*Adnatosphaeridium patulum* sp. nov.

Pl. 24, figs. 1, 2 ; Text-fig. 58

DERIVATION OF NAME. Latin ; *patulus*, spread out, broad.

DIAGNOSIS. Sub-spherical central body with fibrous wall up to 1 μ thick, composed of endocoel and pericoel. Processes intratabular open, flared, with fibrous walls ; one per plate. Adjacent processes united distally. Archaeopyle haplotabular.

HOLOTYPE. B.M.(N.H.) slide V.51977(1). London Clay ; Enborne, sample E 11.

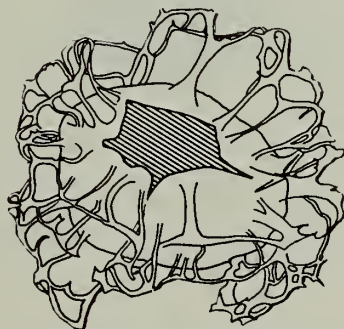


FIG. 57. *Adnatosphaeridium multispinosum* sp. nov. Holotype. Archaeopyle shaded, sulcal notch on the left.

DIMENSIONS. Holotype : diameter of central body 75 by 80 μ . Length of processes up to 37 μ . Observed range : diameter of central body 75–95 μ . Length of processes up to 37 μ . Number of specimens measured, 3.

DESCRIPTION. ?*A. patulum* has a quadrate archaeopyle resulting from the loss of a single plate. The archaeopyle is surrounded by six processes in the holotype ; these may be precingular but until more specimens are studied definite conclusions cannot be drawn. The processes are considerably broader distally than proximally and have undulose margins. Distal margins of adjacent processes are united. The fibres of the process walls are haphazard in orientation. The walls often appear perforate and this may in part be due to differential staining. The central body is medium brown, the processes transparent, yellowish green.

OCCURRENCE. Eocene, London Clay ; Whitecliff, Enborne and Sheppey.

REMARKS. The processes readily distinguish ?*A. patulum* from other described species. Because of the uncertainty with regard to the type of archaeopyle and its shape, the species is tentatively placed in *Adnatosphaeridium*.

OTHER SPECIES

Other species occurring in the London Clay and here referred to the genus *Adnatosphaeridium* are *A. filamentosum* (Cookson & Eisenack 1958), *A. aemulum* (Deflandre 1938), *A. caulleryi* (Deflandre 1938), *A. filiferum* (Cookson & Eisenack 1958), all thought to be derived.

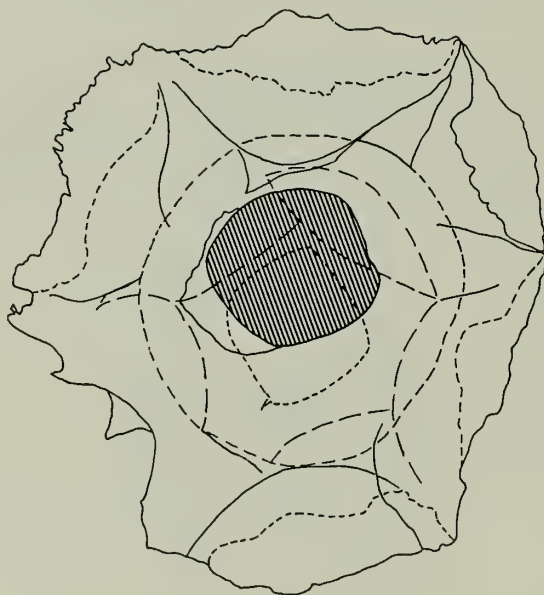


FIG. 58. *Adnatosphaeridium patulum* sp. nov. Holotype. Archaeopyle (haplotabular) is shaded.

Genus **MEMBRANILARNACIA** Eisenack 1963 : 99

EMENDED DIAGNOSIS. Chorate cysts spherical, oval or ellipsoidal, usually thick walled and surrounded by more or less concentric and generally thin walled enveloping membrane supported by processes or supports normal to central body. Processes forked, flared or branched distally. Shafts cylindrical or columnar. Archaeopyle apical.

TYPE SPECIES. *Membranilarnax leptoderma* Cookson & Eisenack 1958. Lower Cretaceous ; Papua.

DISCUSSION. Some of the species originally referred to the genus *Membranilarnax* O. Wetzel (1933) were transferred to *Membranilarnicia* by Eisenack (1963b). Eisenack (1959c) reviewed *Membranilarnax* and showed that the generic description given by O. Wetzel was ambiguous, embodying three distinct groups. These are :

1. Forms with a spherical to oval central body surrounded by a membrane restricted to the equatorial region (pterate cysts). The membrane is supported by processes arising from the central body and branching distally. A pylome (or archaeopyle) has not been observed.
2. Hystrichospheres with a spherical to oval central body surrounded by a concentric outer membrane which is supported by processes arising from the central body. A pylome (archaeopyle) can be present.
3. Hystrichospheres with a central body surrounded by a concentric outer membrane, supported by raised crests, which form polygonal fields on the central body. A pylome can be present.

To the first group can be attributed the type species of *Membranilarnax* (*M. pterospermoides* O. Wetzel). The genus should therefore be restricted to species referable to group 1, but since the structure of the holotype of *M. pterospermoides* cannot be clarified because the specimen is too deeply embedded in a flake of flint and cannot be examined at high magnification, the placing of other species within *Membranilarnax* is not to be recommended.

Eisenack (1963b) erected two new genera according with the second and third types. These are *Membranilarnacia* (corresponding to Group 2), and *Valensiella* (corresponding to Group 3 and synonymous with *Favilarnax* Sarjeant 1963c over which it has seniority). Following Eisenack's abandonment of the name *Membranilarnax*, all residual species left in that genus were provisionally transferred to *Membranilarnacia* by Downie & Sarjeant (1964). Specimens from the London Clay attributable to the genus *Membranilarnacia* possess intratabular processes indicating a reflected tabulation of 1-4', 6", 0-4c, 5"', 1p, 1'''. The archaeopyle is apical with a zigzag margin. From the tabulation and possession of intratabular processes, restricted to one per plate, *Membranilarnacia* must be included in the family Hystrichosphaeridiaceae and cannot therefore be the type genus of the family Membranilarnaciaceae.

Membranilarnacia is distinguished from the genus *Adnatosphaeridium* by having an outer membrane instead of trabeculae, which distally unite the processes of the latter genus. It is possible however that intermediate forms exist.

Membranilarnacia reticulata sp. nov.

Pl. 24, figs. 4-6 ; Text-fig. 59

DERIVATION OF NAME. Latin, *reticulatus*, net-like, netted.

DIAGNOSIS. Ellipsoidal central body with intratabular processes, one per plate. Processes indicating a tabulation of 1-4', 6'', 4c, 5''', 1'''. Cingular processes sometimes absent. Sulcal processes and posterior intercalary process present on some individuals. Processes cylindrical, solid, fibrous, united distally by a fine reticulate membrane totally or partially enclosing central body. Processes rarely exceeding 20 μ in length.

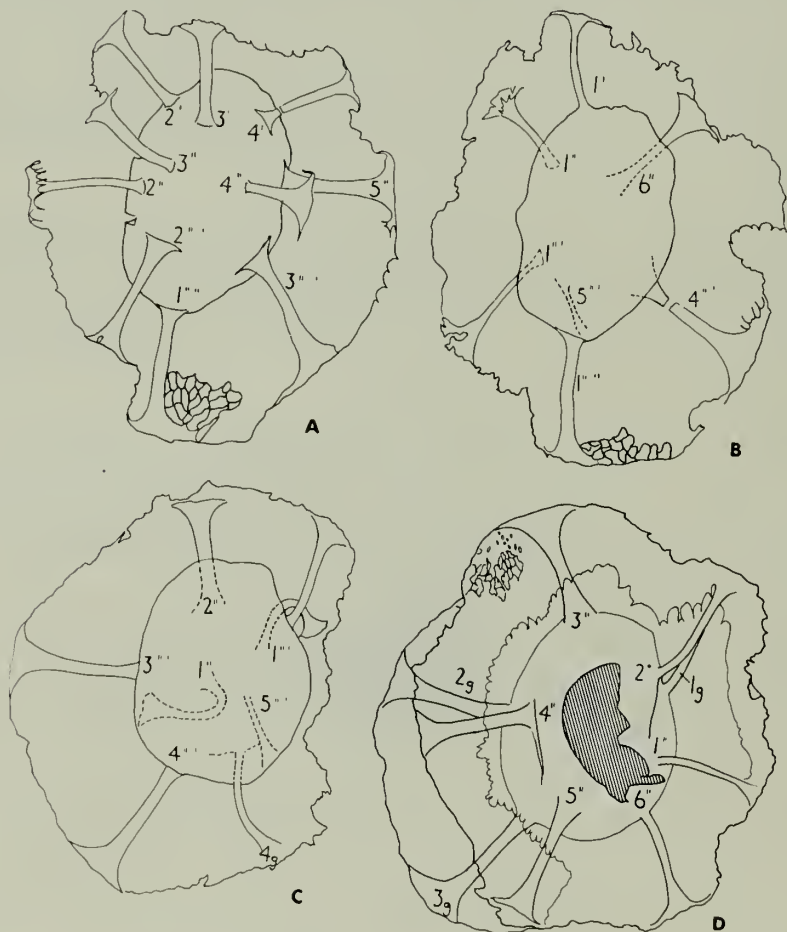


FIG. 59. *Membranilarnacia reticulata* sp. nov. A, Lower (ventral) surface, seen through the upper. Only part of the distal network uniting the processes is shown. B, Upper (dorsal) surface of same specimen. C, Lower (antapical) surface, seen through the upper. D, Upper (apical) surface of same specimen. Archaeopyle shaded, sulcal notch lies between plates 1'' and 6''.

HOLOTYPE. B.M.(N.H.) slide V.51959(2), London Clay ; Sheppey, Kent, sample Sh 1.

DIMENSIONS. Holotype : diameter of central body 42 by 43 μ . Length of processes up to 26 μ . Observed range : diameter of central body 35–44 μ . Length of processes 7–24 μ . Number of specimens measured, 8.

DESCRIPTION. The central body has a thin wall, smooth or slightly granular, comprising the endophragm. When an archaeopyle is present, the zigzag margin sharply delimits six rectangular plates, each bearing a process. The sulcal notch is usually clearly discernible. The process denoting the posterior intercalary plate is more commonly absent.

The fibrous processes rarely exceed two thirds of the diameter of the central body in length. They are generally simple and few in number, this being governed by the number of plates present. The size of the process may be a reflection of its position on the central body, the postcingulars often being smaller than the precingular processes. The cingulum appears to be slightly helicoidal.

The meshwork of the reticulate membrane is variable in size within an individual : it is finer nearer the process. The membrane is not unlike a closely woven net in structure, with numerous fine interconnecting orthogonal threads. The membrane may be restricted to distinct zones as in the figured specimen. There the processes of each series of plates are distally united and have few interconnecting links with processes of other plate series. This can be useful in orientation since it clarifies the position of the different plate series, and particularly the pre- and postcingulars.

Two variants of *M. reticulata* are recognized based on the arrangement of the processes. These are :

Var. *a*. Reflected tabulation as in specific diagnosis but with no cingular processes. Sulcal processes may be present. This is the commoner of the two variants.

Var. *b*. Tabulation as in specific diagnosis with cingular processes present, there being four in number.

Variability in *M. reticulata* also extends to the number of apical processes, some specimens having one, others having four. However since it is impossible to distinguish them when the archaeopyle is developed, the two forms are treated together as parts of the same species.

OCCURRENCE. London Clay ; Whitecliff, Enborne and Sheppey.

REMARKS. Comparison of *M. reticulata* with other described forms suggests close affinity with *Membranilarnax* sp. O. Wetzel (1936), from the Upper Eocene of Germany. Reissinger (1950) figured a similar form which he simply termed a "hystrichosphere", this also being from the Eocene of Germany. Unfortunately neither of these specimens have been preserved, and only Wetzel attempted a description, brief in the extreme, stating that the form was a spiny sphere within an outer shell ; a description too succinct to be useful.

Eisenack (1954b) figured a specimen which he compared with *Membranilarnax* sp., O. Wetzel (1936). Eisenack (1959c) however inferred that the outer membrane

of *M. sp.* does not form a concentric surrounding network but is restricted to an equatorial zone, unlike that in *M. reticulata*. From the illustrations, Reissinger's form looks identical to *M. reticulata*, which often shows a conspicuous absence of the outer membrane in the equatorial zone when cingular processes are absent.

Genus **NEMATOSPHAEROPSIS** Deflandre & Cookson 1955 : 268

EMENDED DIAGNOSIS. Globular to ellipsoidal chorate cysts. Periphragm forms gonal or sutural processes united proximally by sutural ridges or membranes. Adjacent processes distally united by trabeculae. Archaeopyle precingular.

TYPE SPECIES. *Nematosphaeropsis balcombiana* Deflandre & Cookson, 1955. Miocene ; Australia.

DISCUSSION. The tabulation of *Nematosphaeropsis* is identical to that of *Hystri-chosphaera ramosa*.

Nematosphaeropsis balcombiana Deflandre & Cookson

1955. *Nematosphaeropsis balcombiana* Deflandre & Cookson : 268, pl. 8, fig. 5.

DISCUSSION. Two specimens from the London Clay are attributed to *N. balcombiana*. They closely agree with the type material, the dimensions being : central body, length 38–40 μ , breadth 28–33 μ ; process length 10–22 μ . The specimens were found in sample Wh 6 from Whitecliff and E 11 from Enborne.

Genus **CANNOSPHAEROPSIS** O. Wetzel 1932 : 140

EMENDED DIAGNOSIS. Ellipsoidal chorate cyst with precingular archaeopyle and bearing branching or furcate processes like those of *Hystri-chosphaera* in both structure and distribution, but without sutural ridges or septa connecting their bases as in that genus. Processes interconnected distally by trabeculae. Endophragm and periphragm in close contact between bases of processes.

TYPE SPECIES. *Cannosphaeropsis utinensis* O. Wetzel 1932. U. Cretaceous ; Baltic.

DISCUSSION. Evitt (1963) has pointed out that many species included within *Cannosphaeropsis* (according to Deflandre's (1947) definition) significantly differ from the type species. It is therefore proposed to restrict *Cannosphaeropsis* to species possessing gonal and sutural processes allied with a precingular archaeopyle ; species with intratabular processes and apical archaeopyle, formerly attributable to *Cannosphaeropsis*, have been transferred to the genus *Adnatosphaeridium*.

No attempt is made to reallocate species of *Cannosphaeropsis* where the species in question have not been examined.

Cannosphaeropsis reticulensis Pastiels

Pl. 24, fig. 8

1948. *Cannosphaeropsis reticulensis* Pastiels : 49, pl. 5, figs. 7-10.1961. *Cannosphaeropsis reticulensis* Pastiels ; Alberti : 36, pl. 9, fig. 15.

DISCUSSION. Specimens of *C. reticulensis* possessing a precingular archaeopyle with gonal and sutural processes, are present in the London Clay. The interconnecting trabeculae appear to be solid, taeniate and not tubular. The simple acuminate spines arising from the trabeculae of the type material are uncommon in the London Clay forms.

DIMENSIONS. Range observed in London Clay : diameter of central body 26-43 μ , length of processes 9-18 μ . Number of specimens measured, 5.

OCCURRENCE. Eocene, London Clay ; Whitecliff, Enborne and Sheppey. *C. reticulensis* is also known from the Eocene of Belgium (Pastiels 1948) and Germany (Alberti 1961).

Genus *CYCLONEPHELIUM* Deflandre & Cookson 1955 : 285

EMENDED DIAGNOSIS. Chorate cysts with central body flattened dorso-ventrally and apparently concavo-convex, outline circular to slightly oval. Apex and/or antapex with or without blunt prominence, antapex occasionally slightly indented. Ornamentation restricted to circumferential zone of varying width, consisting of (1) processes, of varying lengths and shapes, distinct or more or less confluent, (2) thin membrane supported at intervals by strong processes, or (3) densely arranged surface thickenings. Ornamentation sometimes more strongly developed in antapical region. Archaeopyle apical tetrahedral. Wall layers not distinguished.

TYPE SPECIES. *Cyclonephelium compactum* Deflandre & Cookson 1955. Lower to Upper Cretaceous ; Australia.

DISCUSSION. Tabulation cannot be determined in this genus beyond the fact that there are four apical and six precingular plates. This is apparent from an examination of a detached operculum and the margin of the archaeopyle, which is zigzag.

The shape of specimens of *Cyclonephelium* is variable and is probably partly dependent on subsequent compression in the enclosing sediment. Individuals of the species *C. exuberans* Deflandre & Cookson 1955, are often similar to *Areoligera* in having a convex dorsal surface and a depressed ventral surface. This is not, however, universal, since others appear to have an ellipsoidal outline, both dorsal and ventral surfaces being convex.

Cyclonephelium divaricatum sp. nov.

Pl. 25, fig. 1 ; Text-fig. 60

DERIVATION OF NAME. Latin ; *divaricatus*, spread apart.

DIAGNOSIS. Central body flat or slightly convex with circular outline bearing numerous ambital taeniate processes. Processes united distally in complex

fashion, sometimes by trabeculae, sometimes by perforated membranes. Erect unconnected secæ, acuminate or bifid distally, arising from outer margin of trabeculae or membranes. Length of processes rarely exceeding one-third the diameter of the central body.

HOLOTYPE. B.M.(N.H.) slide V.51956(2). London Clay ; Whitecliff, sample 8.

DIMENSIONS. Holotype : diameter of central body 54 by 71 μ . Observed range : diameter of central body 45–71 μ . Length of processes up to 15 μ . Number of specimens measured, 5.

DESCRIPTION. The central body has a finely reticulate surface and is formed from the extremely thin endophragm. The periphragm gives rise to the taeniate processes. The numerous processes are restricted to the ambitus of the central body save on the precingulars, where the processes surround the archaeopyle margin. The processes are short, with only a few distal interconnctions. They tend to exhibit a linear orientation and are often united proximally. The secæ, arising from the distal margin of the trabeculae or membranes that unite the processes, often appear to be continuations of the processes distally, whilst at other times they arise at points distant from the processes. Occasional simple acuminate processes are present on the central body.

OCCURRENCE. Eocene, London Clay ; Whitecliff, Enborne, Sheppey and Studland.

REMARKS. *C. divaricatum* differs from other described species of *Cyclonephelium* in the nature of the processes distally and the point of origin of the trabeculae or interconnecting membrane.

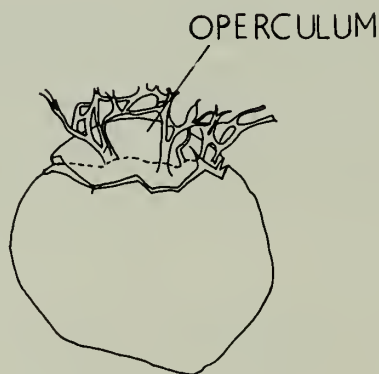


FIG. 60. *Cyclonephelium divaricatum* sp. nov. Partial drawing of specimen showing operculum separating from the test.

Cyclonephelium exuberans Deflandre & Cookson

Text-fig. 61

1948. *Membranilarnax pterospermoides* Pastiels : 46, pl. 5, figs. 11-14.1955. *Cyclonephelium exuberans* Deflandre & Cookson : 281.

DISCUSSION. *C. exuberans* has probably evolved from *C. pastielsi*, intermediate forms between the two being common. Specimens from the London Clay show the same variation in process distribution as *C. pastielsi*, some individuals lacking processes on plates 3" and 6", others having processes on all the precingular plates, although generally with fewer on 3" and 6" than on the others. The prominent sulcal notch lies to the right of the mid-ventral line. The surface of the central body is commonly granular.

DIMENSIONS. Range observed in London Clay : diameter of central body 56-85 μ , length of processes up to 46 μ . Number of specimens measured, 4.

OCCURRENCE. Eocene, London Clay ; Whitecliff and Enborne ; Eocene (Ypresian) of Belgium (Pastiels 1948).

Cyclonephelium ordinatum sp. nov.

Pl. 25, fig. 3 ; Text-fig. 62

DERIVATION OF NAME. Latin ; *ordinatus*, in row, orderly.

DIAGNOSIS. Thin walled central body with granular surface. Processes formed from periphragm and restricted to linear complexes regularly distributed on central



FIG. 61. *Cyclonephelium exuberans* (Pastiels). Partial drawing showing large precingular processes around the margin of the archaeopyle (broken line).

body. Reflected tabulation deduced from linear complexes of 4', 6", 5''', 1p, 1'''''. Processes slender, solid, taeniate, united half to two-thirds along their length by membranes or trabeculae. Processes distally unconnected and unequally bifurcate.

HOLOTYPE. B.M.(N.H.) slide V.51977(2). London Clay; Enborne, Borehole E 11, 61 ft.

DIMENSIONS. Holotype: diameter of central body 61 by 73 μ . Length of processes up to 36 μ . Observed range: diameter of central body 41–74 μ , length of processes up to 40 μ . Number of specimens measured, 4.

DESCRIPTION. This species is unusual in that it possesses processes restricted to the ambitus yet which are grouped into linear or sometimes arcuate complexes reflecting a dinoflagellate tabulation. The apical archaeopyle is nearly always developed and had a clear sulcal notch. The precingulars possess a variable number of processes, plates 1", 2", 4" and 5" having well-developed linear complexes, 3" having a complex of varying extent, whilst 6" can be devoid of processes.

The processes are not unlike those of *Areoligera medusettiformis* (O. Wetzel). The interconnecting membrane sometimes extends to the base of the processes and, if so developed, is often fenestrate proximally. Distally the processes are bifurcate commonly with one fork longer than the other and recurved. Occasionally the processes are acuminate. Branching can occur distally to the interconnecting membrane or trabeculae.

OCCURRENCE. Eocene, London Clay; Whitecliff and Enborne.

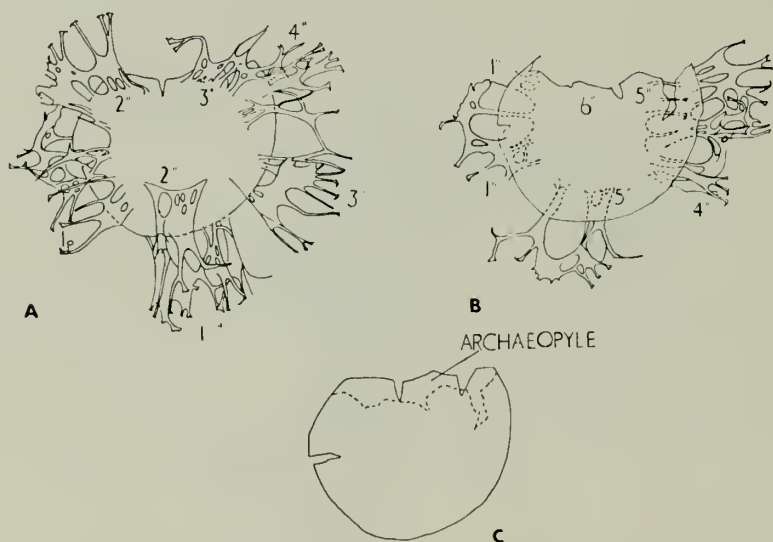


FIG. 62. *Cyclonephelium ordinatum* sp. nov. Holotype. A, Tabulation of the upper (dorsal) surface. B, Tabulation of the lower (ventral) surface seen through the upper. C, Partial drawing to show the ziz-zag nature of the archaeopyle margin.

REMARKS. *C. ordinum* differs from *C. divaricum* in the regular arrangement of the processes in linear complexes and the larger overall size. It is included within the genus *Cyclonephelium* on account of the absence of processes from the mid-dorsal and ventral surface apart from those on the margin of the archaeopyle.

Cyclonephelium pastielsi Deflandre & Cookson

Pl. 25, fig. 2

1948. *Membranilarnax* cf. *liradiscoides* Pastiels : 47, pl. 5, fig. 15.

1955. *Cyclonephelium pastielsi* Deflandre & Cookson : 285.

DISCUSSION. Specimens of *C. pastielsi* from the London Clay almost invariably possess an archaeopyle, apical in position and with a zigzag margin. The prominent sulcal notch lies to the right of the mid-ventral line. Only rarely is a complete individual, with the apex in place, encountered. The numerous, solid taeniate processes are complexly united along their length and distally. They are frequently arranged in linear complexes. Proximally the processes arise singly or in groups of twos or threes. Distally the interconnecting trabeculae may be perforate, up to 5 to 6 μ in width. Unconnected short, slender, acuminate or bifid spines often arise from the trabeculae. Occasional simple acuminate processes occur on the central body.

Pastiels figured a specimen of *C. pastielsi* (as *Membranilarnax* cf. *liradiscoides*, pl. 5, fig. 15) showing an absence of processes round the mid-ventral and mid-dorsal margins of the archaeopyle. In the majority of the London Clay forms the processes are rather more numerous on the ambitus and also completely surround the archaeopyle margin. Those processes round the archaeopyle are more complex in structure than the ambital processes, and are aligned in rows parallel to the margin of the archaeopyle. It is probable that each precingular and postcingular plate has processes to a greater or lesser degree.

Specimens of *C. pastielsi* can have two antapical protuberances, one more strongly developed than the other. When these are present the outline of the central body is closely comparable to that of *Areoligera*. The size of the London Clay forms usually exceeds that of the type material. Transitional forms to *C. exuberans* are not uncommon.

DIMENSIONS. Observed range in London Clay : diameter of central body 43–90 μ , length of processes 12–38 μ . Number of specimens measured, 25.

OCCURRENCE. Common at all horizons of the London Clay. The forms having the larger central bodies are commonest in WC.14, 26 and E.11/88. *C. pastielsi* has also been recorded from the Ypresian of Belgium (Pastiels 1948).

Genus *AREOLIGERA* Lejeune-Carpentier 1938 : 164

EMENDED DIAGNOSIS. Chorate cysts with hemispherical central body, convex dorsal side and flat or depressed ventral side. Processes intratabular, on dorsal surface arranged in soleate or annular complexes, on ventral surface in linear or

occasionally soleate complexes. Plate 1'''' possesses an annular complex. Cingulum indicated by reduced linear complexes. Reflected tabulation of 4', 6'', 2-4c, 5''', 1p, 1'''''. Archaeopyle apical tetratabular. Well developed sulcal notch on ventral surface and lying to right of mid-ventral line. Outline of central body circular with bilobed antapex.

TYPE SPECIES. *Areoligera senonensis* Lejeune-Carpentier 1938b. Upper Cretaceous (Senonian) ; Belgium.

DISCUSSION. Evitt (1961, 1963) has given a full and concise review of the genus. The close relationship to certain species of *Cyclonephelium* has been noted in preceding pages.

Areoligera coronata (O. Wetzel)

Pl. 25, fig. 7

1933. *Hystriosphæra penicillata* forma *coronata* O. Wetzel : 41, pl. 4, fig. 17.

1938. *Areoligera coronata* (O. Wetzel) Lejeune-Carpentier : 168, text-fig. 6.

DISCUSSION. *A. coronata* in the Eocene exhibits considerable variation in the structure of the soleate complexes. Proximally these can be fenestrate or non-fenestrate membranes, with the processes arising from the distal margin of the membrane. Alternatively, the processes may arise directly from the central body and be united along their length by membranes. Distally the slender processes are erect and can be acuminate or bifid. The number of processes per complex is variable. Not infrequently plates 2''' and 4''' have annular and not soleate complexes ; if this is the case, the processes nearest the transverse cingulum are usually shorter. In one individual the processes of adjacent complexes are united distally by trabeculae.

Only plate 6'' never has processes. The apical plates possess four process groups, the smallest of which is that on plate 1'. This is a single taeniate process branched distally. Plates 2' and 3' have tubular annular complexes, diversely branched distally ; these give the impression of having developed from a simple tubular process. Plate 4' has a taeniate process which is branched distally and is intermediate in size between process 1' and processes 2' and 3'.

DIMENSIONS. Range observed in London Clay : diameter of central body, length 53-66 μ , breadth 57-76 μ ; length of processes 10-38 μ . Number of specimens measured, 5.

OCCURRENCE. Eocene, London Clay ; Whitecliff and Sheppey ; Upper Cretaceous of Germany (O. Wetzel 1933).

Areoligera cf. *coronata* (O. Wetzel)

Pl. 25, fig. 5 ; Text-fig. 63

DESCRIPTION. Included here are three specimens which differ from *A. coronata* in having process complexes on all the plates, 6'' having a soleate complex, whilst

plates 1''' and 5''' bear multibranched linear or annular complexes. There are at least four cingular plates and some sulcal plates having linear complexes. The dorsal surface is convex, the ventral surface depressed. The processes on the ventral surface are closer to those of *A. medusettiformis* than those of *A. coronata*, and can be simple or branched distally or proximally.

A. cf. coronata resembles *Systematophora* in having process complexes on both ventral and dorsal surfaces. In the shape of the central body, position of the sulcal notch and predominance of soleate complexes however, it more closely approximates to *Areoligera* with which genus it must be included.

DIMENSIONS. Observed range : diameter of central body 57–71 μ , length of processes up to 27 μ .

OCCURRENCE. Eocene, London Clay ; Sheppey, Kent.

Areoligera cf. medusettiformis (O. Wetzel)

Pl. 25, fig. 4

DESCRIPTION. This has similar processes to *A. medusettiformis* and the same shape of central body. It differs, however, in the presence of process complexes on all the fields and not on the dorsal fields only. The precingular plates bear soleate complexes, whilst plates 1''' and 5''' have annular complexes. The complexes are unusual in being formed partly from simple processes, especially is this so with those processes nearest to the mid-ventral line. There is a well developed right antapical protuberance which is almost in line with the sulcal notch.

DIMENSIONS. Observed range : diameter of central body, 50–67 μ , length of processes up to 3 μ . Number of specimens measured, 2.

OCCURRENCE. Eocene, London Clay ; Sheppey, Kent.



FIG. 63. *Areoligera cf. coronata* (O. Wetzel). Left, upper (ventral) surface ; right, lower (dorsal) surface, viewed through upper. Archaeopyle shaded. GP, girdle processes ; PS, posterior sulcal processes.

Areoligera cf. *senonensis* Lejeune-Carpentier

Pl. 25, fig. 6 ; Text-fig. 64

DESCRIPTION. One beautifully preserved individual from the London Clay of Sheppey, whilst having the distinctive processes of *A. senonensis*, also possesses process complexes on the ventral surface. The excellent preservation enabled the tabulation of 6", 5"', 1_p, 1''' to be determined. The six precingulars bear soleate process complexes, four of the postcingulars, 1''', 2''', 4''' and 5''' bear annular complexes. The single antapical protuberance lies immediately beneath the sulcal notch.

A single archaeopyle operculum possessing four annular complexes can also be attributed to *A. cf. senonensis*. This has an elongate plate 1', with plates 2' and 3' considerably larger than the other two plates.

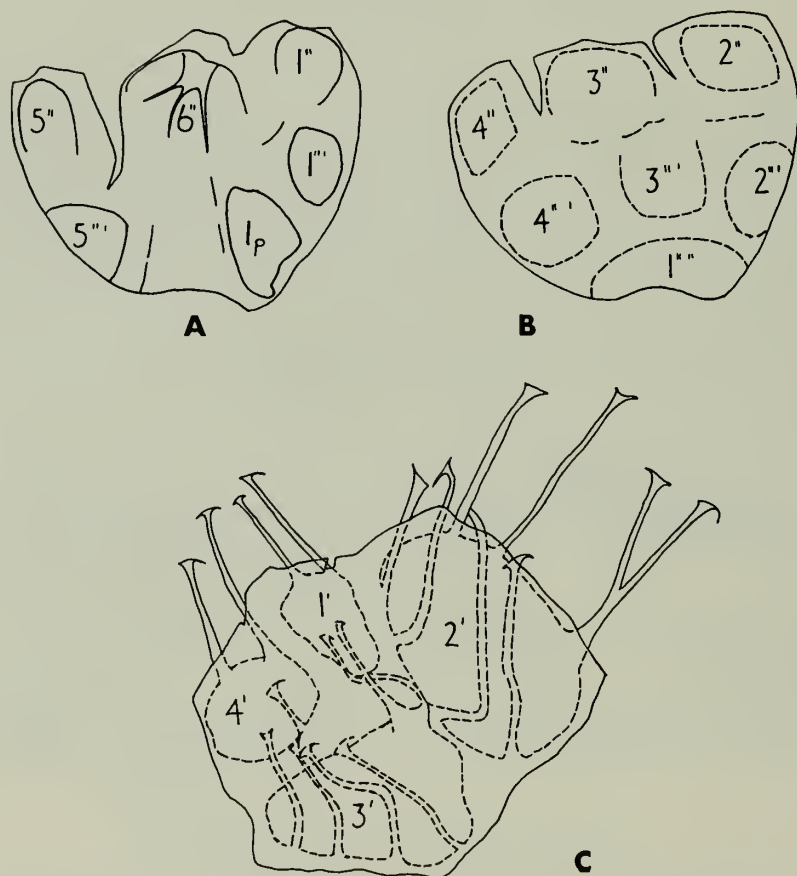


FIG. 64. *Areoligera* cf. *senonensis* Lejeune-Carpentier. A, Tabulation of upper (ventral) surface with processes omitted. B, Tabulation of lower (dorsal) surface seen through the upper. C, An isolated operculum showing its tabulation.

DIMENSIONS. Diameter of central body 70 by 85 μ . Length of processes up to 28 μ .

OCCURRENCE. Eocene, London Clay ; Sheppey, Kent.

REMARKS. *A. cf. senonensis*, like *A. cf. medusettiformis* and *A. cf. coronata* is a form approaching the genus *Systematophora*. The London Clay forms attributed to *Areoligera*, differ from *Systematophora* only because of the presence of process complexes on the central surface, in particular on plate 6" which is usually barren of processes.

Genus **DEFLANDREA** Eisenack 1938 : 187

EMENDED DIAGNOSIS. Cavate cysts with periphragm forming elongate pentagonal (also often somewhat rounded to rhomboidal) outer shell. Lateral walls usually convex. One apical and two antapical horns, more or less reduced. Tabulation, when decipherable, peridinoïd.Periphragm smooth or granular. Cingulum circular longitudinal furrow if observable restricted to hypotract. Inner capsule circular to ovoidal in outline ; endophragm of variable thickness. Archaeopyle intercalary.

TYPE SPECIES. *D. phosphoritica* Eisenack 1938. Oligocene ; East Prussia.

DISCUSSION. The genus *Deflandrea* is represented by a large number of species, some of which clearly overlap. To avoid further confusion, many specimens figured are not given a specific name or detailed description since slight changes in outline of the pericoel are not considered worthy of specific differentiation.

***Deflandrea phosphoritica* subsp. *phosphoritica* Cookson & Eisenack**

Pl. 26, figs. 2, 3, 6, 9

1961b. *Deflandrea phosphoritica* subsp. *phosphoritica* Cookson & Eisenack : 39.

DISCUSSION. This subspecies, common in the London Clay, often possesses a clearly marked indented circular cingulum and a sulcus restricted to the hypotract and widening posteriorly. The outline of the periphragm varies from being identical to the type material to closely approaching *Deflandrea phosphoritica* subsp. *australis* Cookson & Eisenack 1961, which has a more granular periphragm and a short solid cylindrical process at the distal extremity of the apical horn and frequently more pronounced antapical horns.

A few specimens without a capsule were observed ; in one the interior was empty, in the others formless organic matter appeared to have formed from decay of the capsule.

The archaeopyle of the London Clay specimens of *D. phosphoritica* subsp. *phosphoritica* is always intercalary in the periphragm but appears to occupy a more apical position in the endophragm. The granules on the surface of the periphragm often delimit plate boundaries and also tend to show linear alignment, running from the apex towards the antapex.

DIMENSIONS. Observed range in London Clay : outer shell, length 110–133 μ , breadth 75–103 μ ; capsule, length 55–75 μ , breadth 66–86 μ . Number of specimens measured, 13.

OCCURRENCE. Eocene, London Clay ; Whitecliff, Enborne, Sheppey and Studland. Also from the Palaeocene to the Oligocene in Europe and the Lower Tertiary of Australia.

Deflandrea phosphoritica subsp. *australis* Cookson & Eisenack

Pl. 26, fig. 4

1961b. *Deflandrea phosphoritica* subsp. *australis* Cookson & Eisenack, pl. 1, figs. 2, 3.

DISCUSSION. Only three specimens from the London Clay can be definitely attributed to *D. phosphoritica* subsp. *australis*, although intermediate forms to *D. phosphoritica* subsp. *phosphoritica* are common.

DIMENSIONS. Observed range in London Clay : outer shell, length 138–157 μ , breadth 72–104 μ , capsule, length 69–75 μ , breadth 52.6–87 μ .

OCCURRENCE. Eocene, London Clay ; Enborne and Sheppey. Also occurs in the Lower Tertiary of Australia (Cookson & Eisenack 1961b).

Deflandrea denticulata Alberti

1948. *Peridinium* cf. *galeatum* (pars.) Pastiels : 50, pl. 5, figs. 17–20.

1959. *Deflandrea denticulata* Alberti ; 102, text-fig. 1.

DISCUSSION. The London Clay specimens attributable to *D. denticulata* are generally smaller than the type material and are sufficiently well preserved to give details of tabulation, determinable from the small acuminate or blunt processes that occasionally delimit the plate boundaries. These indicate the presence of four apical, three anterior intercalary, five postcingular, and as yet unknown numbers of precingular and antapical plates. The archaeopyle is intercalary, resulting from the loss of plate 2a. The tabulation of *D. denticulata* is thus peridinoid. The small processes, often longer on the prominent apical and antapical horns, are not restricted to the plate boundaries. They have a tendency to be orientated in linear complexes running in an antero-posterior direction. The sutures of the indented sulcus are always denticulate.

DIMENSIONS. Range in London Clay : outer shell, length 72–126.5 μ , breadth 43–74 μ ; capsule, length 37–64 μ ; breadth 38–61 μ , length of apical horn 20–39 μ . Number of specimens measured, 15.

OCCURRENCE. Eocene, London Clay ; Whitecliff, Enborne and Sheppey. Also recorded from the Palaeocene to the Lower Eocene in Germany (Alberti 1959b), and from the Ypresian in Belgium (Pastiels 1948).

Deflandrea oebisfeldensis Alberti

Pl. 26, fig. 1

1959b. *Deflandrea oebisfeldensis* Alberti : 95. pl. 8, figs. 10-13.

DISCUSSION. Two specimens from the London Clay are positively identified as *D. oebisfeldensis* ; one of them does not possess a capsule.

OCCURRENCE. Eocene, London Clay ; Enborne and Sheppey. Recorded also from the Palaeocene to the Lower Eocene in Germany and from Stalingrad, Russia (Alberti 1959b).

Deflandrea wardenensis sp. nov.

Pl. 26, fig. 5

DERIVATION OF NAME. From Warden Point, Sheppey, Kent.

DIAGNOSIS. Cavate cysts, sub-circular to ovoidal periphragm, one apical and two short antapical horns. Conical apical horn merging imperceptibly into lateral walls; two antapical horns more positively delimited and straight or slightly diverging. Length of antapical horns approximately equal. Thin walled ovoidal capsule, closely appressed to periphragm except at horns. Surface of periphragm has short acuminate or blunt processes, not restricted to sutures of cingulum and sulcus. Archaeopyle common.

HOLOTYPE. B.M.(N.H.) slide V.51980(1). London Clay ; Sheppey, Kent. sample 2.

DIMENSIONS. Holotype : periphragm, length 57μ , breadth 46μ ; capsule, length 36μ , breadth 43μ . Observed range : periphragm, length $46-64\mu$, breadth $43-50\mu$, capsule, length $33-41\mu$, breadth $40-46\mu$. Number of specimens measured, 6.

DESCRIPTION. The epitract is longer than the hypotract. In outline the former is conical with convex lateral sides, the latter is rounded with the antapical horns being sharply delimited. All three horns can be acuminate but are more commonly blunt. The antapical horns are well separated. The equatorial and longitudinal furrows are both wide with the latter broadening posteriorly. Five postcingulars have been discerned ; the rest of the tabulation is too difficult to decipher.

OCCURRENCE. Eocene, London Clay ; Sheppey, Whitecliff and Enborne.

REMARKS. Species of *Deflandrea* having processes on the sutures of the cingulum, sulcus and plate boundaries are *D. denticulata* ; *D. echinoidea* Cookson & Eisenack 1958 (Upper Cretaceous ; Australia) ; and *D. spinulosa* Alberti 1959 (Oligocene ; Germany). All these have distinctive outlines which readily distinguish them from *D. wardenensis*.

Genus *THALASSIPHORA* Eisenack & Gocht 1960 : 51

EMENDED DIAGNOSIS. Pterate cysts with spherical to ellipsoidal central body, smooth or more commonly granular. Periphragm in form of helmet-shaped "lamellar wing" and in contact with endophragm only on dorsal surface of central body. Archaeopyle precingular.

TYPE SPECIES. *Bion pelagicum* Eisenack 1938. Oligocene ; East Prussia.

DISCUSSION. *Thalassiphora* Eisenack & Gocht is now considered to be referable to the Dinophyceae (Downie, Evitt & Sarjeant 1963) on account of the frequently occurring archaeopyle. As Alberti (1961) noted, the structure of *Thalassiphora* resembles that of *Pterospermopsis* superficially but detailed examination shows that in the former, the periphragm is attached to the endophragm on one surface of the central body only, the dorsal surface. The periphragm extends considerably beyond the central body as a wing lamella, in shape resembling an inverted basin with the margin often turned over. The position of the archaeopyle is constantly dorsal anterior, the keel when present, is posterior. If an archaeopyle is present, it occurs in the periphragm and endophragm. Free opercula are often encountered in sample.

In *Pterospermopsis*, the wing lamella is in contact with the central body along an "equatorial zone" only. Species of *Pterospermopsis* do not possess an archaeopyle.

Thalassiphora pelagica (Eisenack)

Pl. 26, fig. 7

1938. *Bion pelagicum* Eisenack : 187.

1954. *Pterospermopsis pelagica* (Eisenack) Eisenack : 71, pl. 12, figs. 17, 18.

1960. *Thalassiphora pelagica* (Eisenack) Eisenack & Gocht : 513, text-figs. 1-3.

1961. *Pterospermopsis pelagica* (Eisenack) ; Gerlach : 209, pl. 28, fig. 15.

1963. *Thalassiphora pelagica* (Eisenack) ; Gerlach : 50, pl. 3, fig. 3.

1963. *Thalassiphora pelagica* (Eisenack) ; Brosius : 50, pl. 3, fig. 3.

DISCUSSION. *T. pelagica* is characterized by the presence of a keel on the periphragm. In the London Clay, orientation of the specimens has been guided by the position of the archaeopyle, which forms by the loss of a single precingular plate. The archaeopyle is anterior in position, the keel always being posterior with respect to this. The face of the central body containing the archaeopyle is dorsal. The archaeopyle is present in the periphragm and endophragm and has a convex triangular outline. Specimens with the operculum lying within the central body have been observed. The ovoidal central body has a wall up to 1.5μ thick. The thick periphragm is fibrous with a reticulate ornamentation ; it can be perforate. In size, the London Clay forms show close agreement with the type material.

DIMENSIONS. Range observed in London Clay ; overall diameter $170-220\mu$; central body $85-107\mu$; archaeopyle $30-42\mu$; keel 13μ . Number of specimens measured, 6.

OCCURRENCE. Eocene, London Clay ; Sheppey, Kent, and from the Upper Eocene to Middle Miocene of Germany.

Thalassiphora delicata sp. nov.

Pl. 26, fig. 8

DERIVATION OF NAME. Latin ; *delicatus*, tender, dainty.

DIAGNOSIS. A *Thalassiphora* with ellipsoidal central body possessing a smooth thin wall. Periphragm in form of wing lamella, delicate, often irregularly folded and turned over on its margin. No keel present.Periphragm can be perforate. An archaeopyle may be present.

HOLOTYPE. B.M.(N.H.) slide V.51756(3). London Clay ; Enborne, sample E 11.

DIMENSIONS. Holotype : diameter of central body 34 by 43 μ , overall diameter 74 by 75 μ . Observed range : diameter of central body 34–57 μ , overall diameter 74–120 μ . Number of specimens measured, 4.

DESCRIPTION. *T. delicata* exhibits considerable variation in width of the periphragm, this is partly due to unequal folding. Some of the folds on the periphragm suggest the presence of a cingulum ; this is however difficult to visualise since the periphragm does not completely surround the central body. Both the endophragm and periphragm are thin.

REMARKS. This is only the third species allocated to this genus. It differs from the other two in size, the extremely thin periphragm and endophragm, the commonly perforate periphragm and the absence of a keel.

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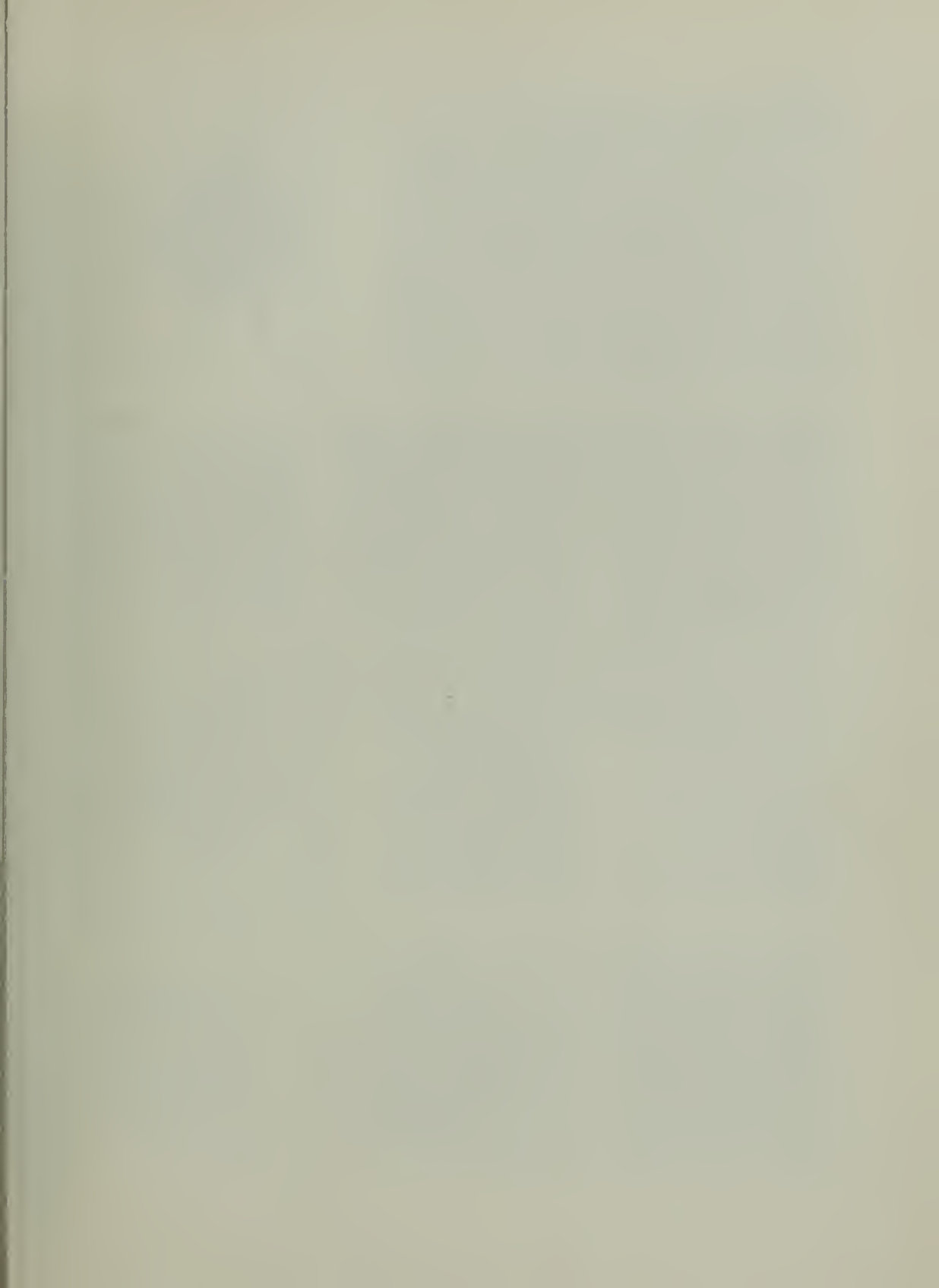


PLATE 1

FIG. 1. *Hystrichosphaera ramosa* (Ehrenberg) var. *ramosa* nov. Holotype. Slide xxv. Flint from Delitzsch. Humboldt-Universität, Berlin. $\times 400$.

FIGS. 2, 3. *Hystrichosphaera ramosa* var. *reticulata* nov. Holotype. PF.3038(1). $\times 500$. Fig. 3. Surface reticulation in focus. $\times 1250$.

FIG. 4. *Hystrichosphaera ramosa* var. *multibrevis* nov. Cenomanian (boring depth, 670 feet). PF.3040(2). $\times 500$.

FIG. 5. *Hystrichosphaera ramosa* var. *gracilis* nov. Cenomanian (boring depth, 670 feet). PF.3040(3). $\times 500$.

FIG. 6. *Hystrichosphaera ramosa* var. *ramosa* nov. Cenomanian (boring depth, 730 feet). P.F.3033(3). $\times 500$.

FIG. 7. *Hystrichosphaera crassipellis* Deflandre & Cookson. PF.3033(2). $\times 500$.

FIG. 8. *Hystrichosphaera crassipellis* Deflandre & Cookson. Cenomanian (boring depth, 770 feet). Wall section to illustrate the unusual thickness. FM.770(1). $\times 975$.

FIG. 9. *Hystrichosphaera cingulata* (O. Wetzel). PF.3039(1). $\times 500$.

FIG. 10. *Hystrichosphaera cingulata* var. *reticulata* nov. PF.3039(2). $\times 500$.

FIG. 11. *Hystrichosphaera crassimurata* sp. nov. Holotype, PF.3040(1). $\times 500$.

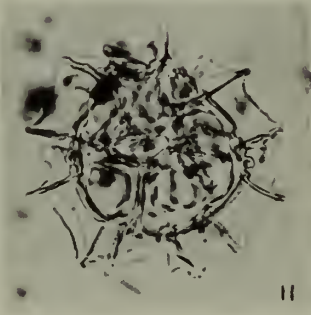
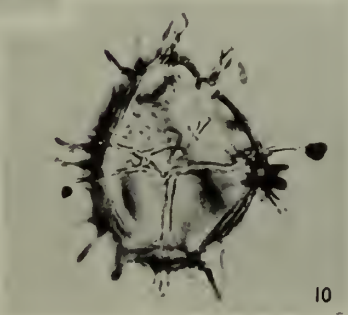
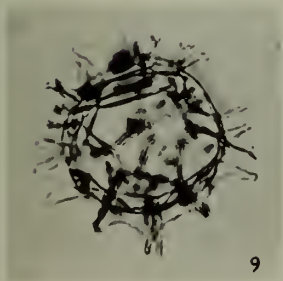
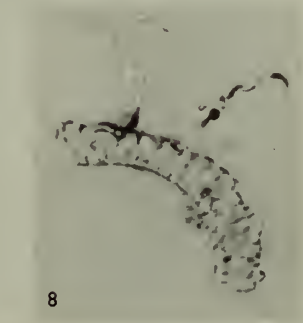
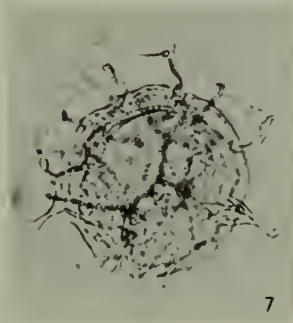
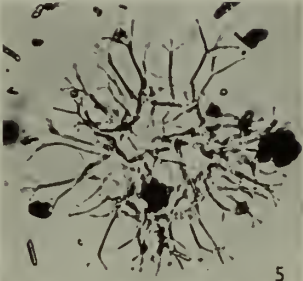
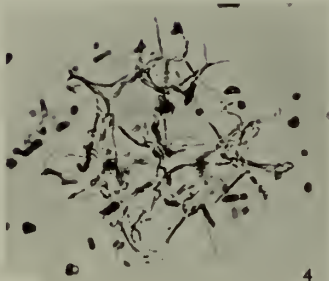
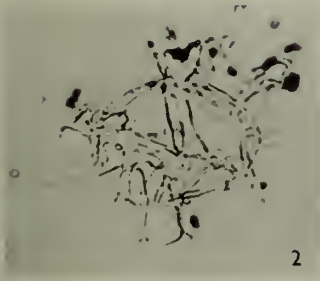
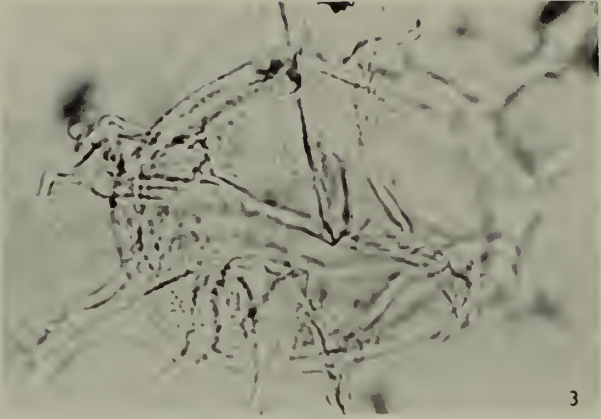
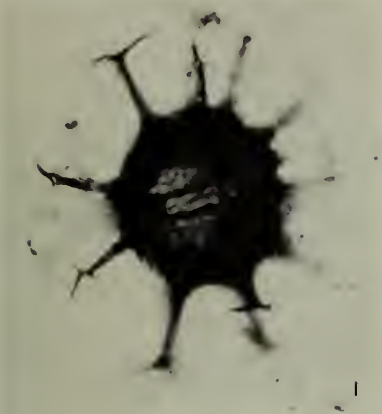


PLATE 2

FIGS. 1, 2. *Achomosphaera sagera* sp. nov. Holotype. PF.3041(1). Precingular archaeopyle shown. $\times 500$. Fig. 2. Surface reticulation in focus. $\times 1250$.

FIG. 3. *Achomosphaera ramulifera* (Deflandre). Cenomanian (boring depth, 840 feet). Precingular archaeopyle shown. FM.840(1). $\times 500$.

FIG. 4. *Hystrichosphaera cingulata* var. *reticulata* nov. Cenomanian (boring depth, 730 feet). Lateral view, archaeopyle towards the north-west. PF.3039(2). $\times 5000$.

FIG. 5. *Cleistosphaeridium flexuosum* sp. nov. Holotype, PF.3045(1). $\times 500$ (phase contrast).

FIG. 6. *Cleistosphaeridium heteracanthum* (Deflandre & Cookson). PF.3041(2). Cenomanian (boring depth, 650 feet). Complete specimen showing form of processes. $\times 500$ (phase contrast).

FIG. 7. *Cleistosphaeridium heteracanthum* (Deflandre & Cookson). Cenomanian (boring depth, 840 feet). FM.840/9. $\times 500$.

FIGS. 8-10. *Exochosphaeridium phragmites* gen. et sp. nov. 8, Cenomanian (boring depth, 810 feet). Apical process and cingular processes present. PF.3043(1). $\times 500$. 9, 10 Holotype, PF.3035(3). Precingular archaeopyle to the north-west and apical process to the south-west. $\times 500$.

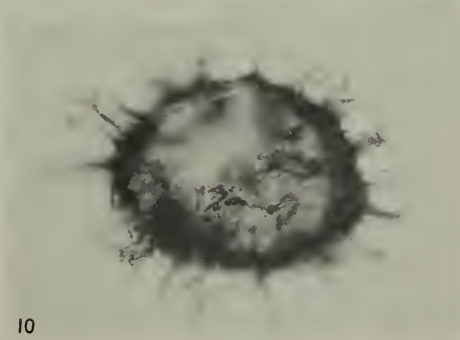
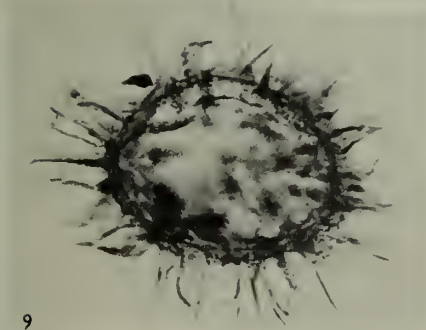
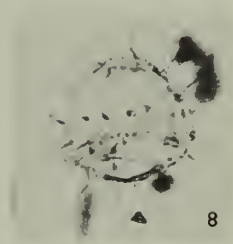
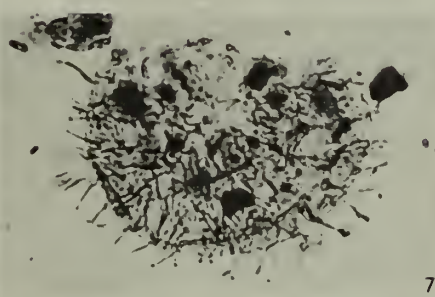
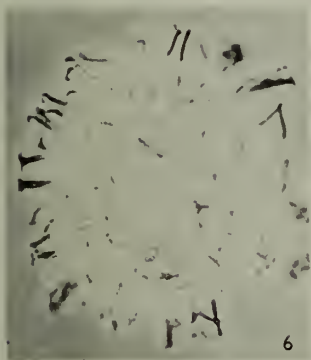
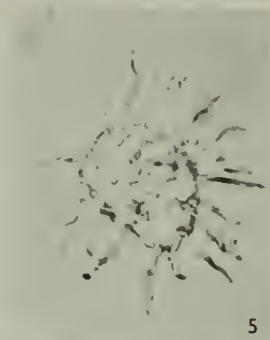
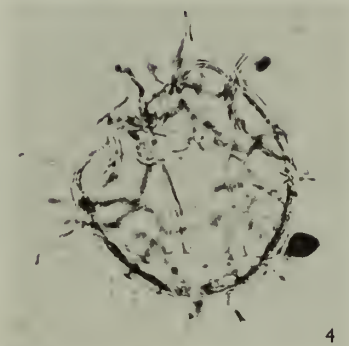
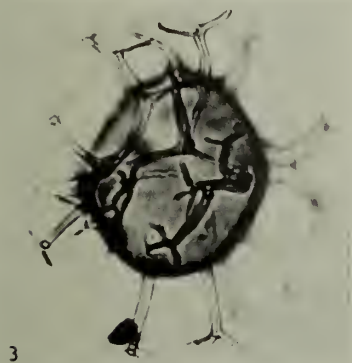
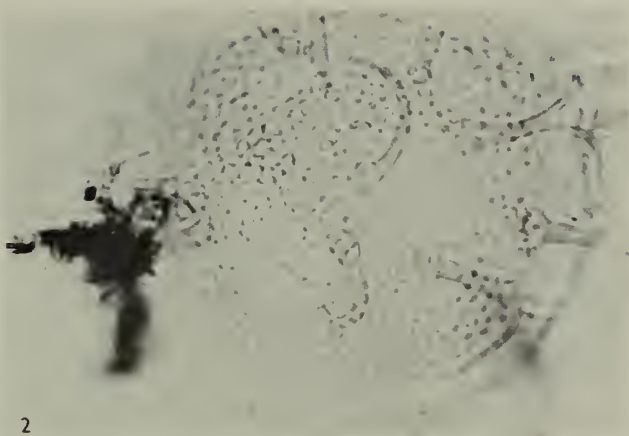
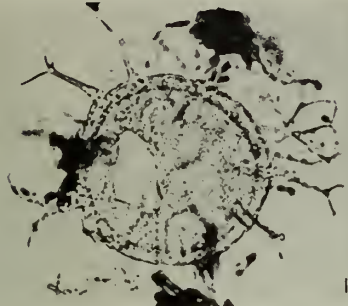


PLATE 3

- FIG. 1. *Hystrichosphaera ramosa* var. *ramosa* nov. Upper Oxfordian, Throstler Clay. V.51714(1). $\times 500$.
- FIG. 2. *Prolixosphaeridium deirense* gen. et sp. nov. Holotype, V.51727(2). $\times 500$.
- FIG. 3. *Tanyosphaeridium regulare* sp. nov. Holotype, V.51755(1). $\times 500$.
- FIG. 4. *Cordosphaeridiosum cracenospinosum* sp. nov. Holotype, V.51748(1). $\times 200$.
- FIG. 5. *Perisseiasphaeridium pannosum* gen. et sp. nov. London Clay; Enborne boring (at 43.25 feet depth). E.11/71/9. $\times 525$.
- FIG. 6. *Cordosphaeridium multispinosum* sp. nov. Holotype, V.51751(1). $\times 500$.
- FIG. 7. *Achomosphaera neptuni* (Eisenack). V.51716(1). $\times 500$.
- FIG. 8. *Cordosphaeridium gracilis* (Eisenack). V.51746(1). $\times 312$.
- FIG. 9. *Cordosphaeridium inodes* (Klumpp). V.51745(1). Apical view. $\times 500$.

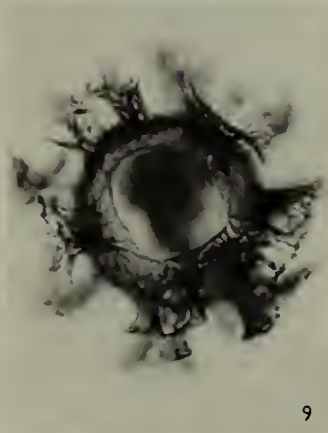
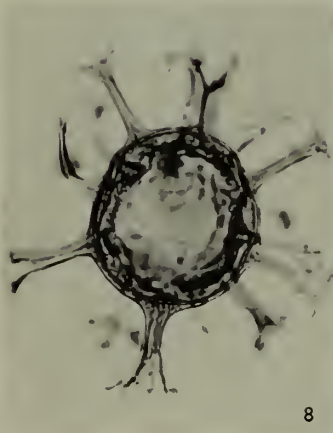
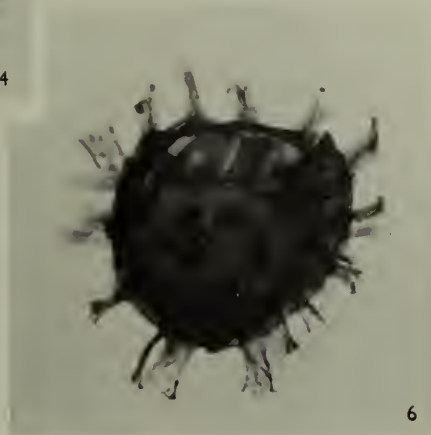
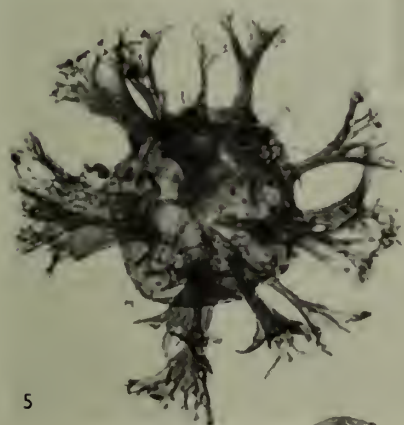
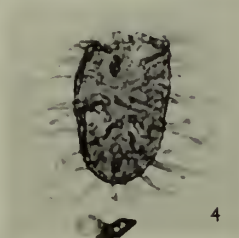
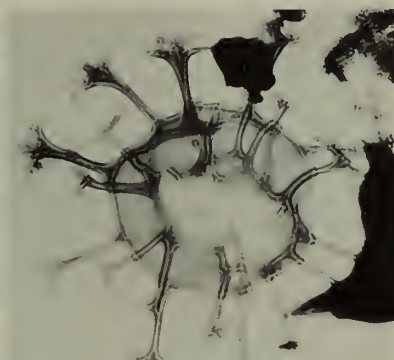
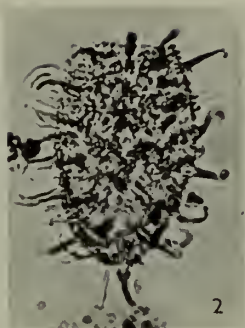
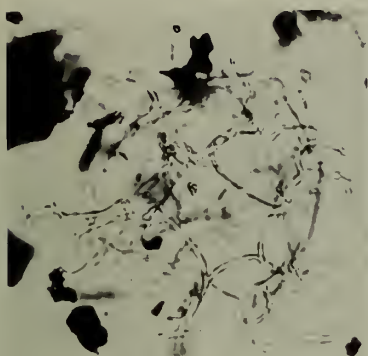


PLATE 4

- FIG. 1. *Hystrichosphaera buccina* sp. nov. Holotype, V.51761(1). $\times 400$.
 FIG. 2. *Diphyes colligerum* (Deflandre & Cookson). V.51754(1). $\times 500$.
 FIG. 3. *Diphyes colligerum* (Deflandre & Cookson). London Clay; (85 feet above base of London Clay) Sheppey. Sh.3/1(1). Apical archaeopyle to the north-west. $\times 500$.
 FIG. 4. *Hystrichosphaera ramosa* var. *granomembranacea* nov. Holotype, V.51759(1). $\times 500$.
 FIG. 5. *Hystrichosphaera cornuta* var. *laevimura* nov. Holotype, V.51752(3). $\times 500$.
 FIG. 6. *Hystrichosphaera ramosa* var. *multibreva* nov. Holotype, V.51758(1). $\times 500$.
 FIG. 7. *Hystrichosphaera cornuta* Gerlach. V.51741(2). $\times 550$.
 FIG. 8. *Hystrichosphaera ramosa* var. *membranacea* (Rossignol). Membrane well developed on the apical pole. London Clay (173 feet above base of London Clay); Sheppey, Kent. Micropalaeont. Lab. Colln., University of Sheffield. $\times 375$.
 FIG. 9. *Hystrichosphaera ramosa* var. *granosa* nov. Holotype, V.51752(2). $\times 500$.
 FIG. 10. *Polysphaeridium pastielsi* sp. nov. Holotype, V.51753(1). $\times 425$.
 FIG. 11. *Homotryblum tenuispinosum* gen. et sp. nov. An isolated plate bearing a single intratabular process. London Clay; Enborne boring (at 53 feet depth). E.11/61/5(1). $\times 750$.
 FIG. 12. *Hystrichosphaera ramosa* var. *membranacea* (Rossignol). V.51747(2). $\times 500$.

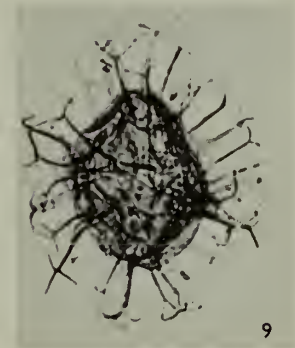
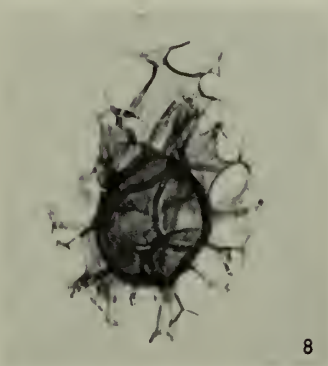
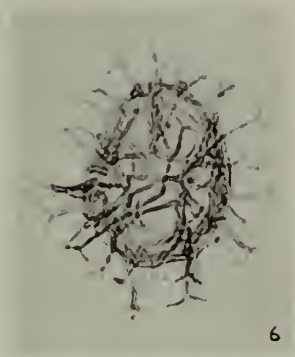
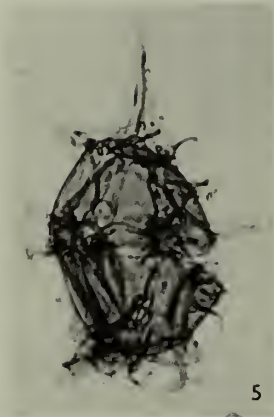
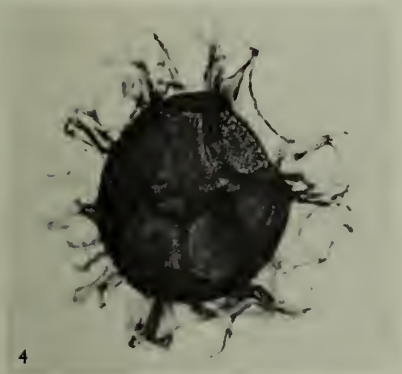
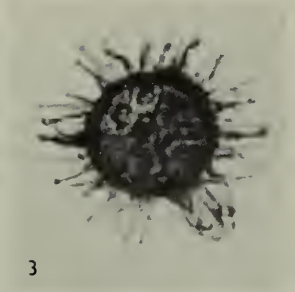
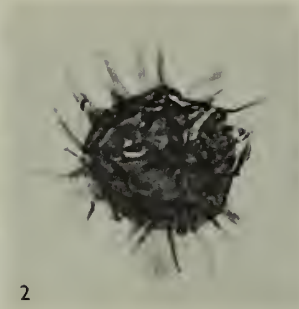
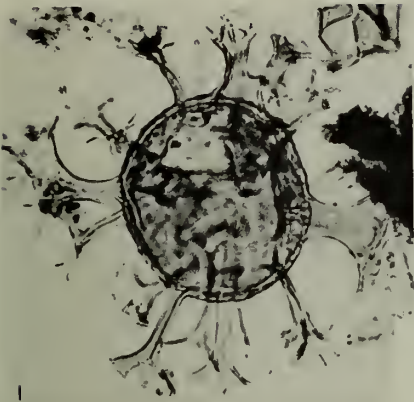
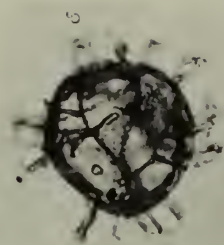


PLATE 5

- FIG. 1. *Achomosphaera ramulifera* var. *perforata* nov. London Clay ; Enborne (boring depth, 83.25 feet). Note precingular archaeopyle. WC.3/6(1). $\times 425$.
- FIG. 2. *Hystrichosphaera monilis* sp. nov. Holotype, V.51763(1). $\times 500$.
- FIG. 3. *Achomosphaera alcicornu* (Eisenack). V.51765(1). $\times 425$.
- FIG. 4. *Achomosphaera ramulifera* var. *perforata* nov. Holotype, V.51764(1). $\times 475$.
- FIG. 5. *Cordosphaeridium fibrospinosum* sp. nov. Holotype, V.51747(1). $\times 475$.
- FIG. 6. *Hystrichosphaera ramosa* var. *gracilis* nov. Holotype, V.51757(1). $\times 350$.
- FIG. 7. *Hystrichosphaera perforata* sp. nov. Holotype, V.51760(1). $\times 550$.
- FIG. 8. *Cordosphaeridium latispinosum* sp. nov. Holotype, V.51746(2). $\times 640$.



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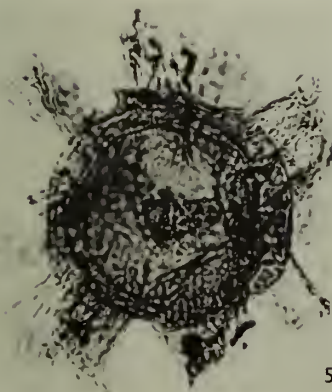
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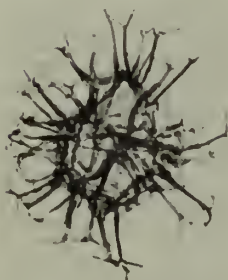
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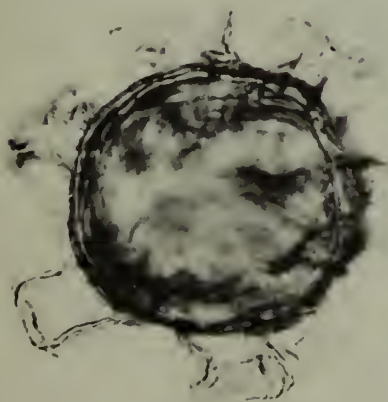
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PLATE 6

FIG. 1. *Hystrichosphaeridium tubiferum* (Ehrenberg). Holotype. Slide XXV. Flint from Delitzsch. Humboldt-Universität, Berlin. Apical view. $\times 400$.

FIG. 2. *Hystrichosphaeridium tubiferum* (Ehrenberg). Holotype. Medial view. $\times 400$.

FIG. 3. *Hystrichosphaeridium readei* sp. nov. Holotype, PF.3030(2). $\times 500$.

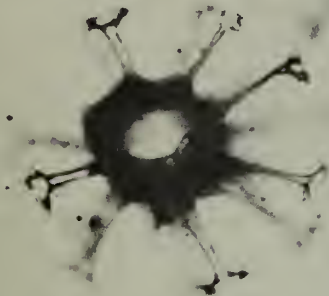
FIG. 4. *Hystrichosphaeridium deanei* sp. nov. Cenomanian (borehole depth, 690 feet). FM.690/12(2). $\times 400$.

FIG. 5. *Cleistosphaeridium ancoriferum*. Cenomanian (borehole depth, 810 feet). PF.3044(1). $\times 500$.

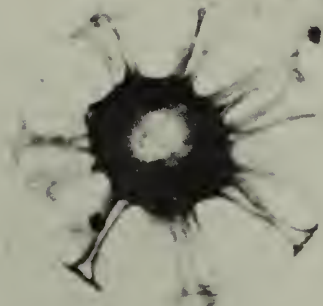
FIG. 6. *Hystrichosphaeridium mantelli* sp. nov. Holotype, PF.3032(1). $\times 500$.

FIG. 7. *Tanyosphaeridium variecalamum* gen. et sp. nov. Holotype, PF.3035(2). $\times 500$.

FIG. 8. *Hystrichosphaeridium deanei* sp. nov. Holotype, PF.3030(1). $\times 500$.



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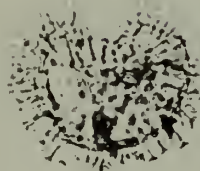
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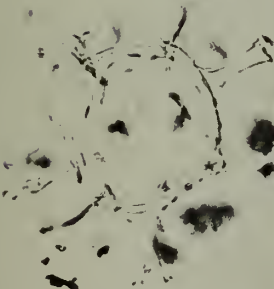
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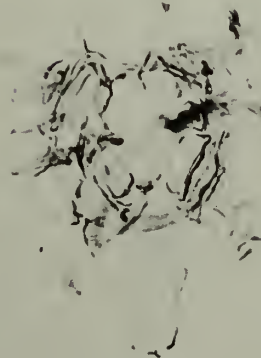
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PLATE 7

FIG. 1. *Oligosphaeridium complex* (White). Neotype, lateral view. PF.3034(1).
× 500.

FIG. 2. *Oligosphaeridium complex* (White). Cenomanian (borehole depth, 840 feet).
Lateral view PF.3035(5). × 500.

FIG. 3. *Polysphaeridium pumilum* sp. nov. Holotype, PF.3037(1). × 975.

FIG. 4. *Polysphaeridium pumilum* sp. nov. Cenomanian (borehole depth, 770 feet).
FM.770/7(1). × 975.

FIG. 5. ?*Cordosphaeridium fasciatum* sp. nov. Holotype, V.51719(1). × 975.

FIG. 6. ?*Cordosphaeridium fasciatum* sp. nov. Holotype. Nature of fibrous periph-
ragm well shown. × 975.

FIG. 7. *Litosphaeridium siphoniphorum* (Cookson & Eisenack). Cenomanian (borehole
depth 750 feet). Apical view showing 6-sided archaeopyle surrounded by 6 precingular pro-
cesses. PF.3037(3). × 500.

FIG. 8. *Litosphaeridium siphoniphorum* (Cookson & Eisenack). Cenomanian (bore hole
depth, 770 feet). Antapical view. FM.770/1(1). × 500.

FIG. 9. *Hystrichosphaeridium radiculatum* sp. nov. Cenomanian (borehole depth, 690
feet). PF.3030(3). × 500.

FIG. 10. *Oligosphaeridium reticulatum* sp. nov. Holotype, lateral view, PF.3035(1).
× 500.



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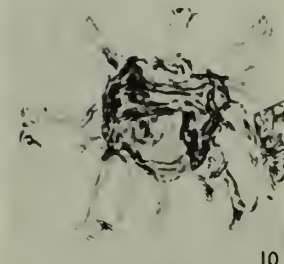
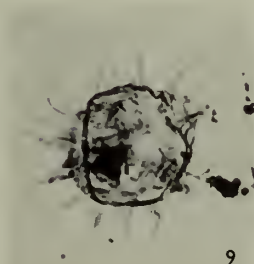
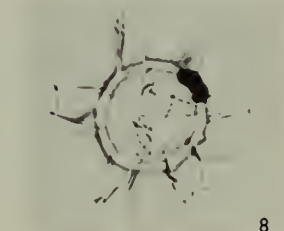
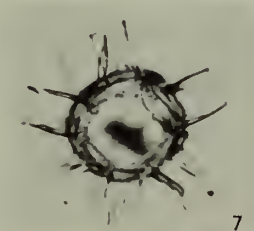
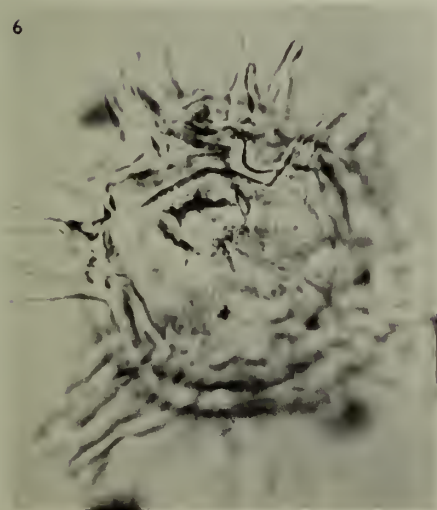
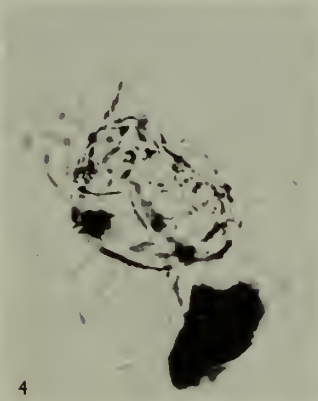
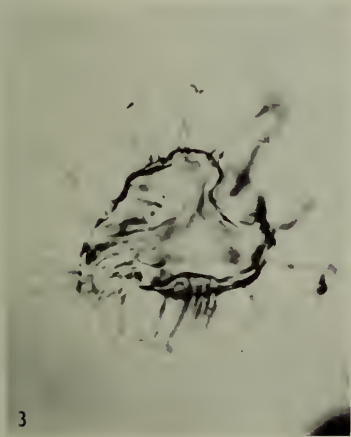


PLATE 8

FIG. 1. *Hystrichosphaeridium bowerbanki* sp. nov. Cenomanian (borehole depth, 750 feet). FM.750/2(1). $\times 500$.

FIG. 2. *Oligosphaeridium prolixispinosum* sp. nov. Cenomanian (borehole depth, 750 feet). PF.3037(2). $\times 500$.

FIG. 3. *Oligosphaeridium prolixispinum* sp. nov. Holotype, PF.3036(1). $\times 500$.

FIG. 4. *Hystrichosphaeridium bowerbanki* sp. nov. Holotype, PF.3033(1). $\times 500$.

FIG. 5. *Hystrichosphaeridium tubiferum* (Ehrenberg). Cenomanian (borehole depth, 690 feet). FM.690/12(1). $\times 500$.

FIG. 6. *Hystrichosphaeridium radiculatum* sp. nov. Holotype, PF.3031(1). $\times 500$.

FIG. 7. *Surculosphaeridium longifurcatum* (Firtion). Cenomanian (borehole depth, 730 feet). Antapical view. FM.730/2(1). $\times 500$.

FIG. 8. *Polysphaeridium laminaspinosum* sp. nov. Holotype, PF.3052(1). $\times 975$. (Phase contrast).

FIG. 9. *Callaiosphaeridium asymmetricum* (Deflandre & Courteville). Cenomanian (boring depth, 840 feet). Medial view in focus to show 6 large tubular cingular processes. FM.840/6(1). $\times 500$.

FIG. 10. Antapical view of same showing 5 postcingular processes. $\times 500$.

FIG. 11. *Surculosphaeridium longifurcatum* (Firtion) PF.3042(1) Cenomanian (boring depth, 840 feet). Lateral view showing 3 series of processes—precingular, cingular and postcingular. $\times 500$.

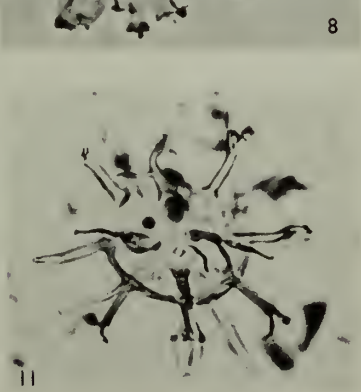
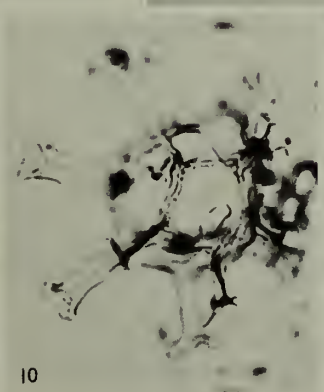
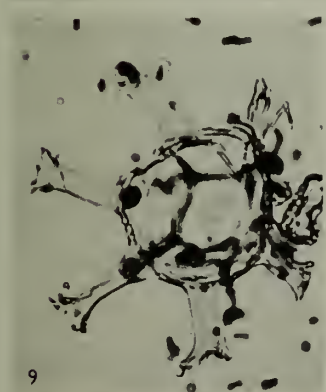
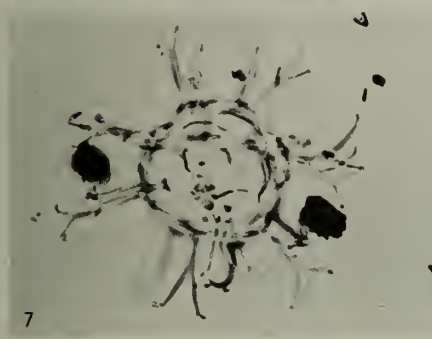
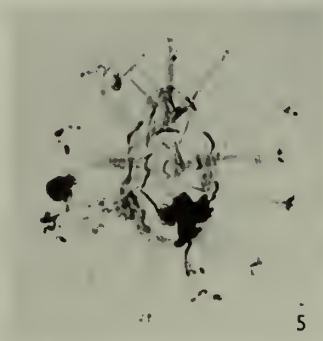
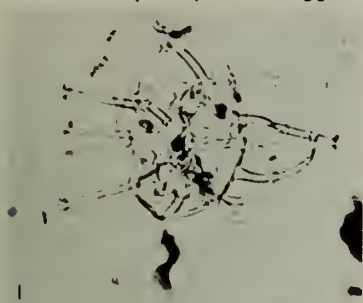


PLATE 9

FIG. 1. *Cleistosphaeridium ancoriferum* (Cookson & Eisenack). Cenomanian (boring depth, 690 feet). Detached 6-sided apical region. FM.690/4(1). $\times 1250$. (Phase contrast).

FIG. 2. *Callaiosphaeridium asymmetricum* (Deflandre & Courteville). Speeton Clay (at 10.325 metres depth). V.51716(2). $\times 500$.

FIG. 3. *Hystrichosphaeridium simplicispinum* sp. nov. V.51729(2). $\times 500$.

FIG. 4. *Oligosphaeridium macrotubulum* (Neale & Sarjeant). Holotype, V.51712(2). $\times 400$.

FIG. 5. *Hystrichosphaeridium arborispinum* sp. nov. Speeton Clay (at 42.5 feet depth). V.51719(3). $\times 500$.

FIG. 6. *Surculosphaeridium cribrotubiferum* (Sarjeant). Holotype, V.51735(1). $\times 500$.

FIG. 7. *Oligosphaeridium vasiformum* (Neale & Sarjeant). Holotype, V.51709(1). $\times 400$.

FIG. 8. *Surculosphaeridium vestitum* (Deflandre). V.51736(1). $\times 500$.

FIG. 9. *Hystrichosphaera* sp. V.51724(1). $\times 500$.

FIG. 10. *Hystrichosphaeridium arborispinum* sp. nov. Holotype, V.51727(3). Lateral view. $\times 500$.

FIG. 11. *Achomosphaera neptuni* (Eisenack). V.51717(1). Precingular archaeopyle to the north. $\times 500$.

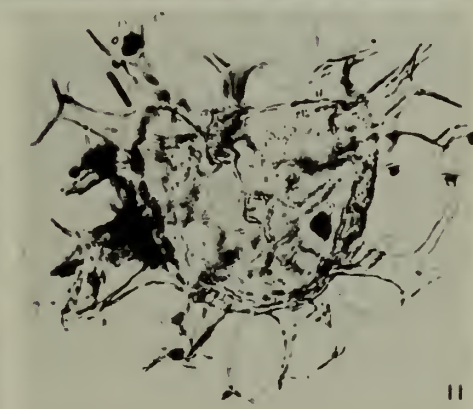
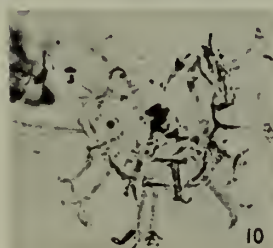
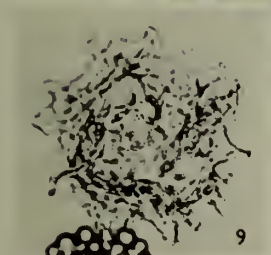
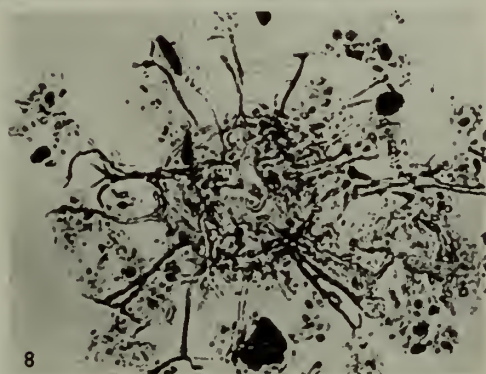
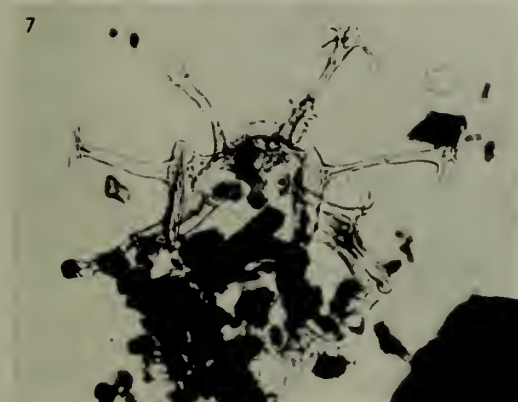
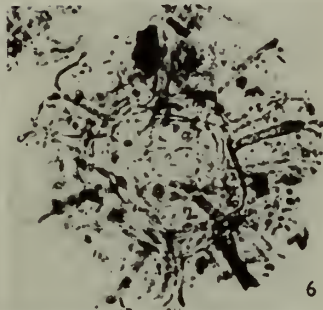
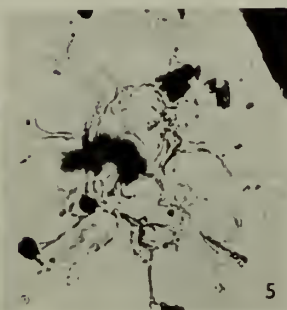
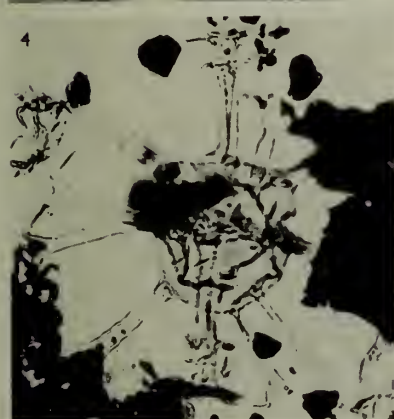
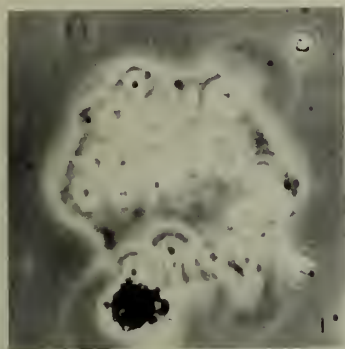


PLATE 10

FIG. 1. *Oligosphaeridium vasiformum* (Neale & Sarjeant). Holotype, V.51709(3). Two precingular processes missing. $\times 400$.

FIG. 2. *Hystrichosphaeridium tubiferum* (Ehrenberg). London Clay ; (5 feet above base of London Clay) Sheppey. Sh.1/2(1). $\times 425$.

FIG. 3. *Oligosphaeridium complex* (White). London Clay ; (146 feet above base of London Clay) Whitecliff Bay. Apical archaeopyle (sutural notch to the west) surrounded by 6 precingular processes. WC.16/1(1). $\times 425$.

FIG. 4. *Hystrichosphaeridium costatum* sp. nov. Holotype, V.51708. $\times 500$.

FIG. 5. *Hystrichosphaeridium patulum* sp. nov. Holotype, V.51739(1). $\times 1250$.

FIG. 6. *Hystrichosphaeridium salpingophorum* (Deflandre). V.51734(1). $\times 500$.

FIG. 7. *Cleistosphaeridium diversispinosum* gen. et sp. nov. Holotype, V.51750(1). $\times 400$.

FIG. 8. *Hystrichosphaeridium latirictum* sp. nov. Holotype, V.51740(1). $\times 975$.

FIG. 9. *Oligosphaeridium pulcherrimum* (Deflandre & Cookson). London Clay (78 feet above base of London Clay); Sheppey. Positions of the processes well shown, the absence of cingular processes being noticeable. Sh.2/5(1). $\times 875$.

FIG. 10. *Hystrichosphaeridium tubiferum* var. *brevispina* nov. Holotype, V.51738(1). $\times 500$.

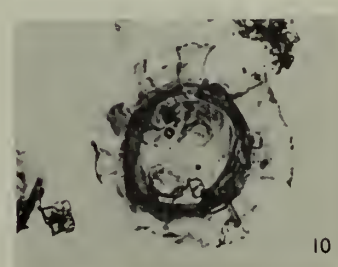
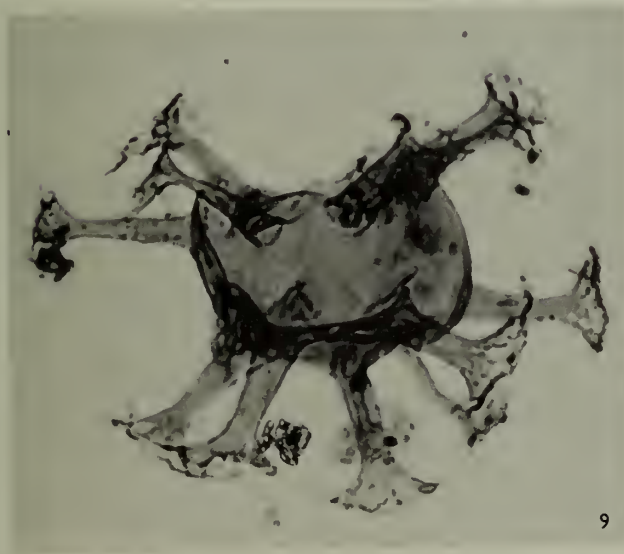
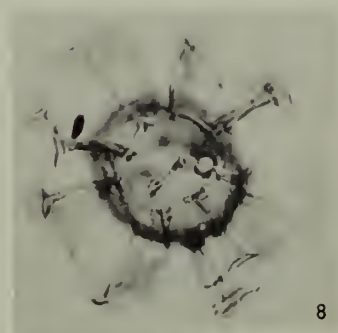
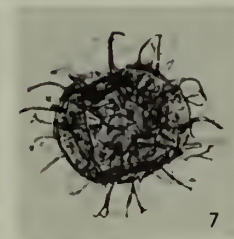
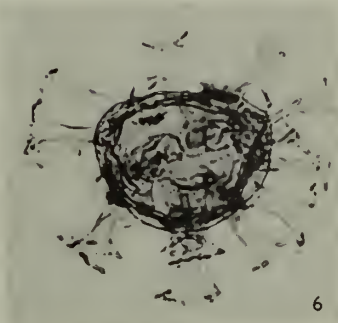
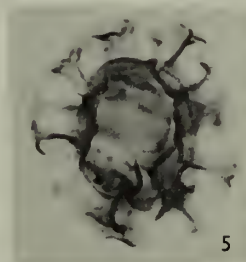
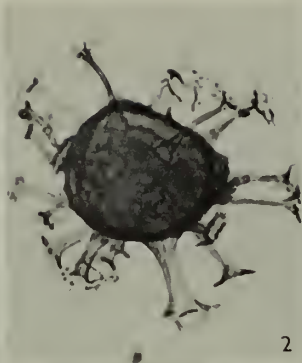
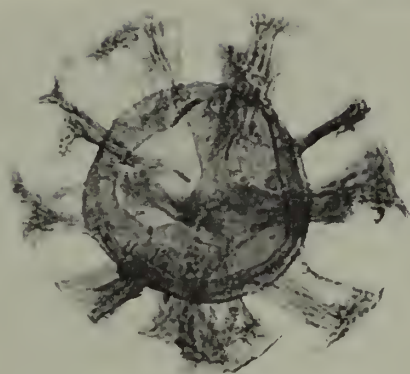
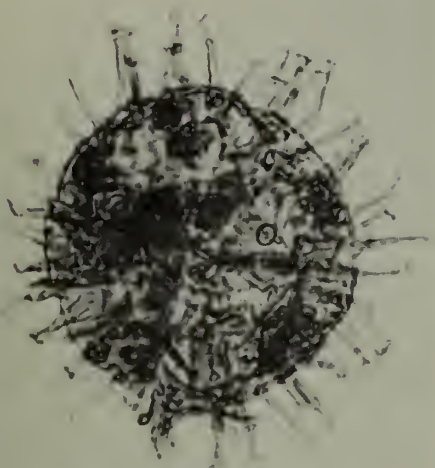


PLATE 11

- FIG. 1. *Polysphaeridium subtile* gen. et sp. nov. Holotype, V.51752(1). $\times 850$.
- FIG. 2. *Cordosphaeridium exilimurum* sp. nov. London Clay (275 feet above base of London Clay); Whitecliff Bay. Archaeopyle well shown. V.51749(1). $\times 425$.
- FIG. 3. *Hystrichosphaeridium sheppeyense* sp. nov. Holotype, V.51741(1). $\times 850$.
- FIG. 4. *Cordosphaeridium gracilis* (Eisenack). London Clay (731 feet above base of London Clay); Sheppey. Detached apical plate. Sh.5/1(1). $\times 450$.
- FIG. 5. *Oligosphaeridium pulcherrimum* (Deflandre & Cookson). V.51742(1). Operculum only slightly displaced and bearing 4 apical processes.
- FIG. 6. *Cordosphaeridium gracilis* (Eisenack). London Clay (173 feet above base of London Clay); Sheppey. Haplotabular archaeopyle well shown. V.51746(3). $\times 400$.
- FIG. 7. *Cordosphaeridium gracilis* (Eisenack). London Clay (173 feet above base of London Clay); Sheppey. Detached apical plate showing characteristic shape. Sh.5/1(2). $\times 450$.
- FIG. 8. *Perisseiasphaeridium pannosum* gen. et sp. nov. Holotype, V.51743(1). $\times 500$.
- FIG. 9. *Cleistosphaeridium disjunction* sp. nov. Holotype, V.51739(2). $\times 400$.



2

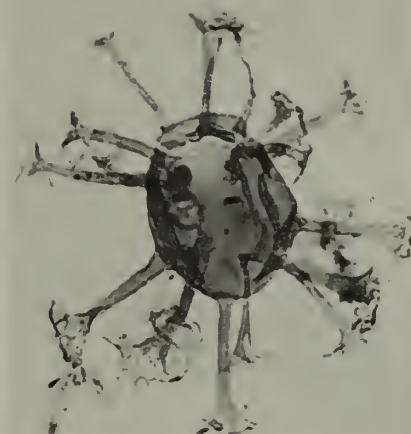
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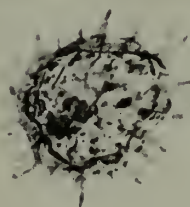
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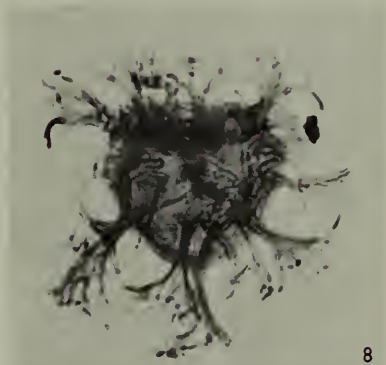
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PLATE 12

FIG. 1. *Homotryblum tenuispinosum* sp. nov. London Clay ; Enborne (boring depth, 53 feet). Complete specimen showing medial rupture. V.51756(3). $\times 500$.

FIG. 2. *Cordosphaeridium divergens* (Eisenack). London Clay ; Whitecliff, Isle of Wight. V.51750(1). $\times 500$.

FIG. 3. ?*Litosphaeridium inversibuccinum* sp. nov. Holotype, V.51744(1). Archaeopyle shown. $\times 975$.

FIG. 4. *Homotryblum pallidum* sp. nov. London Clay ; Enborne (boring depth, 53 feet). Epitracial operculum bearing apical and precingular processes. V.51759(5). $\times 700$.

FIG. 5. *Homotryblum tenuispinosum* sp. nov. Holotype, V.51756(1). $\times 700$.

FIG. 6. *Homotryblum pallidum* sp. nov. Holotype, V.51756(1). $\times 800$.

FIG. 7. *Homotryblum tenuispinosum* sp. nov. London Clay (78 feet above base of London Clay) ; Sheppey. Enlargement of part of the epitract to show that it is composed of a number of polygonal plates, each bearing a single intratabular process. V.51759(4). $\times 1200$.

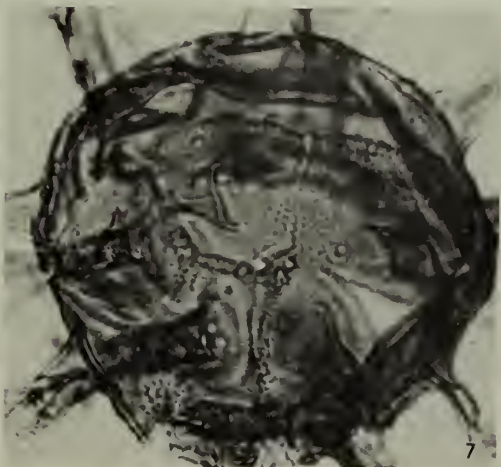
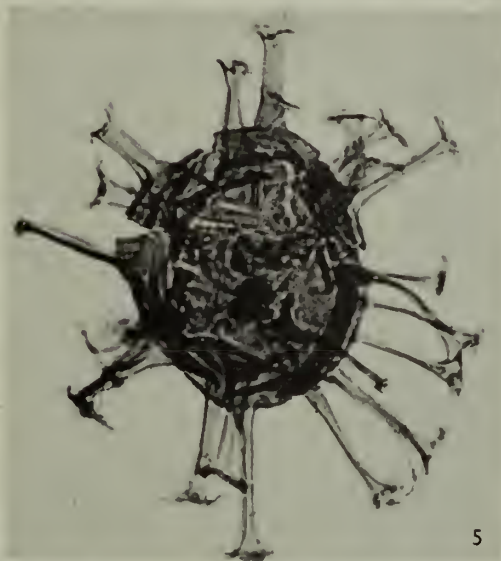
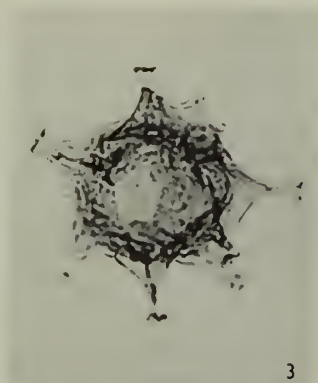


PLATE 13

Gonyaulacysta gongylos sp. nov.

FIG. 1. Ventral surface of holotype, V.51708(1). $\times 500$.

FIG. 2. Dorsal surface of holotype viewed by transparency. $\times 500$.

Gonyaulacysta palla sp. nov.

FIG. 3. Ventral surface of holotype, V.51718(2). $\times 500$.

FIG. 4. Dorsal surface of holotype. $\times 500$.

Gonyaulacysta aichmetes sp. nov.

FIG. 5. Ventral surface of holotype, V.51730(2). $\times 500$.

FIG. 6. Dorsal surface of holotype. $\times 500$.

Gonyaulacysta helicoidea (Eisenack & Cookson)

FIG. 7. Ventral surface of specimen, V.51718(1). $\times 500$.

FIG. 8. Dorsal surface of same, viewed by transparency. $\times 500$.

Gonyaulacysta episoma sp. nov.

FIG. 9. Ventral surface of holotype, V.51730(1).

FIG. 10. Dorsal surface of holotype, viewed by transparency. $\times 500$.

Gonyaulacysta axicerastes sp. nov.

FIG. 11. Ventral surface of holotype, V.51727(1). $\times 500$.

FIG. 12. Dorsal surface of holotype, viewed by transparency. $\times 500$.

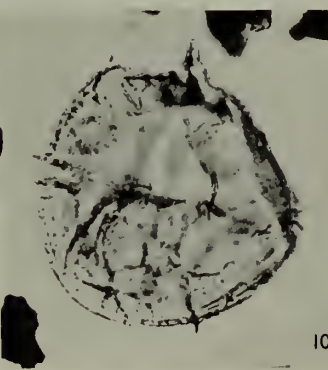
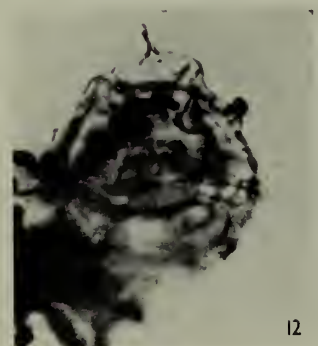
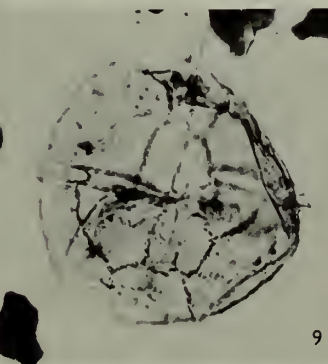
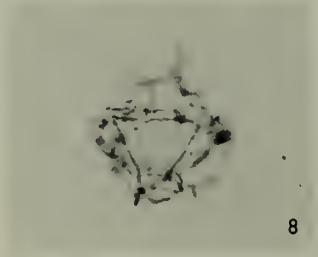
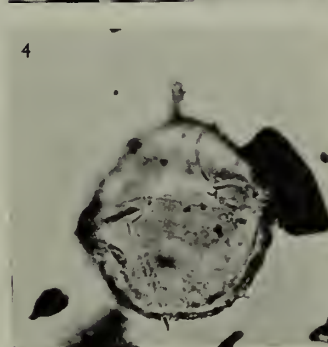
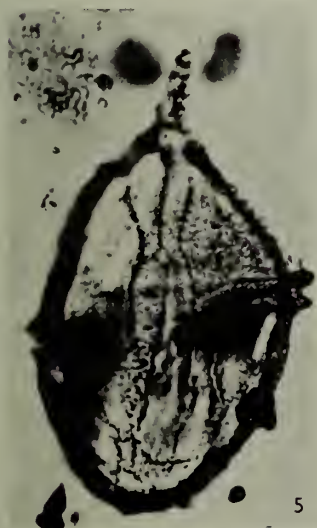
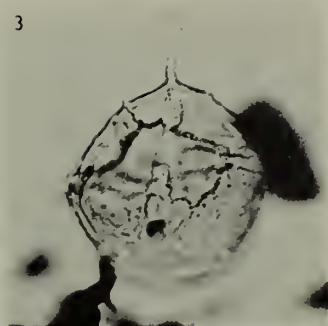
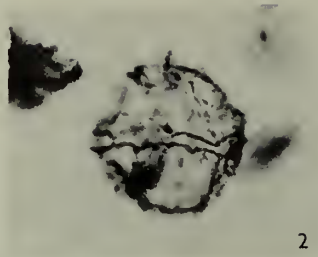
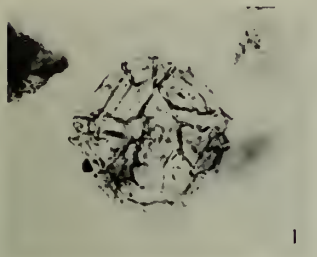


PLATE 14

Gonyaulacysta hadra sp. nov.

FIG. 1. Dorsal surface of the holotype, V.51731(1). The archaeopyle cover is within the shell. $\times 500$.

Gonaulacysta whitei sp. nov.

FIG. 2. Ventral surface of the holotype, PF.3048(1).

Gonyaulacysta cassidata (Eisenack & Cookson)

FIG. 3. Ventral surface of specimen PF.3047(1), viewed by transparency. $\times 500$.

FIG. 4. Dorsal surface of same. $\times 500$.

Gonyaulacysta orthoceras (Eisenack)

FIG. 5. Ventral surface of specimen, V.51730(3). $\times 500$.

FIG. 6. Dorsal surface of same, viewed by transparency. $\times 500$.

Psaligonyaulax deflandrei gen. et. sp nov.

FIG. 7. Ventral surface of the holotype, PF.3049(1). $\times 500$.

FIG. 8. Dorsal surface of same, viewed by transparency. $\times 500$.

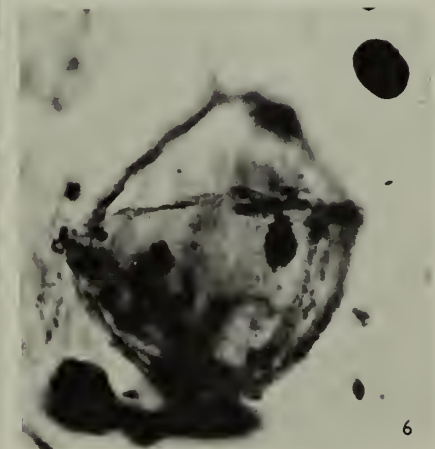
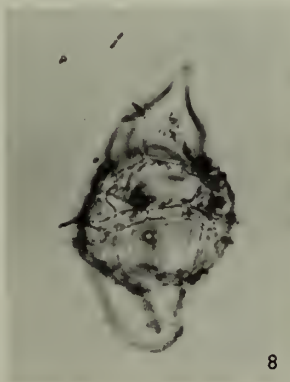
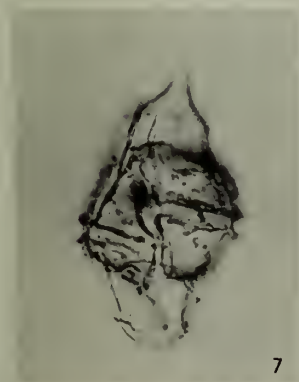
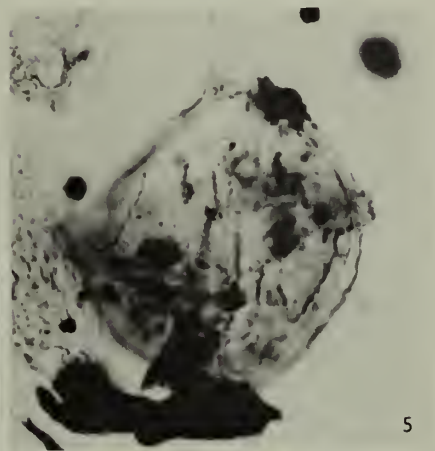
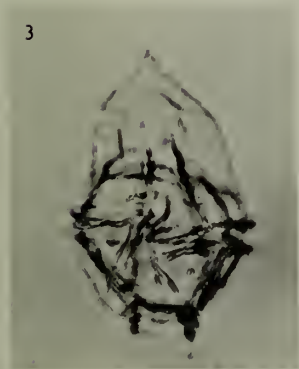
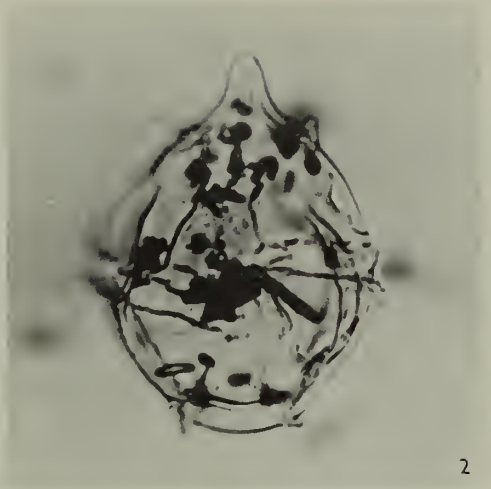
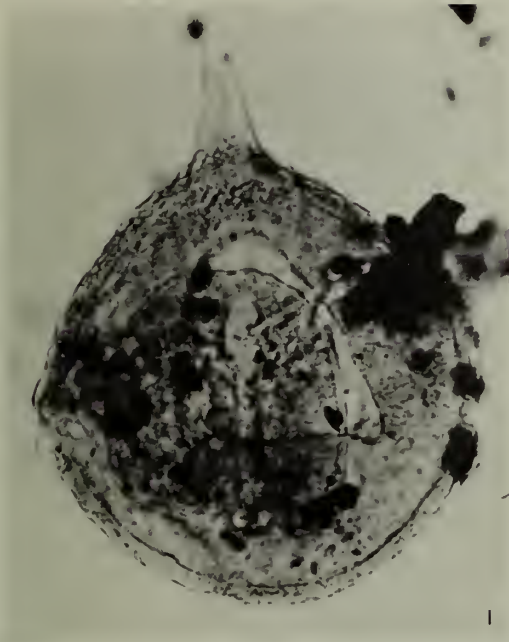


PLATE 15

Gonaylacysta fetchamense sp. nov.

FIG. 1. Ventral surface of holotype, PF.3046(1). $\times 500$.

FIG. 2. Dorsal surface of same, viewed by transparency. $\times 500$.

Leptodinium alectrolophum sp. nov.

FIG. 3. Ventral surface of paratype, V.51725(1). $\times 500$.

FIG. 4. Dorsal surface of same, viewed by transparency. $\times 500$.

FIG. 5. Oblique view of dorsal surface of holotype, V.51735(1). $\times 500$.

FIG. 6. Oblique view by transparency of the ventral surface of same. $\times 500$.

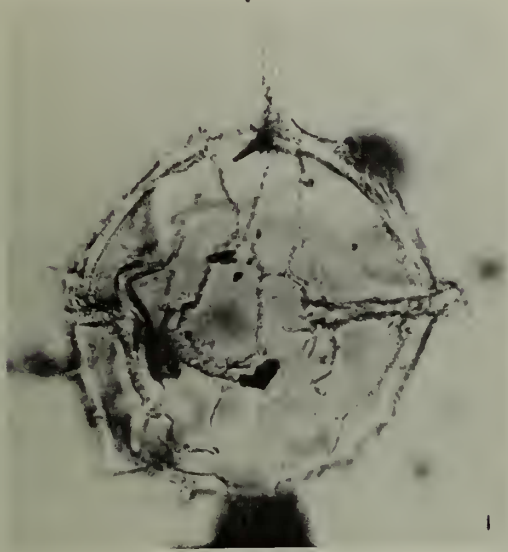
Meiourogonyaulax valensii gen. et sp. nov.

FIG. 7. Ventral surface of holotype. B.S.60 (Laboratoire de Micropaléontologie, École Pratique des Hautes Études, Paris). Photo. by Prof. G. Deflandre, reproduced by his permission. $\times c. 700$.

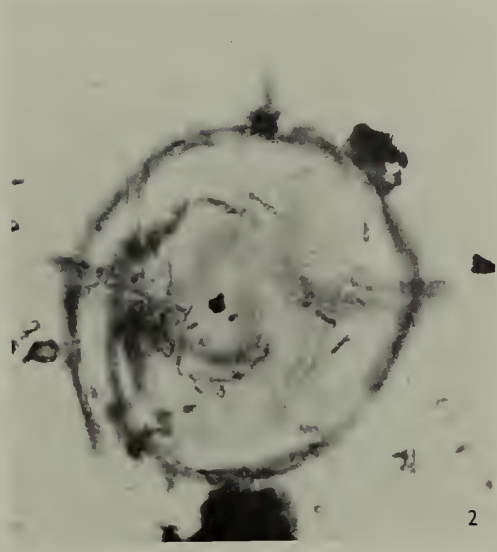
Gonyaulacysta helicoidea (Eisenack & Cookson)

FIG. 8. Specimen, V.51728(1), in oblique ventral view. $\times 500$.

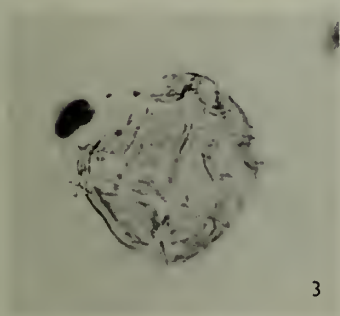
FIG. 9. The same specimen, in oblique dorsal view, by transparency. $\times 500$.



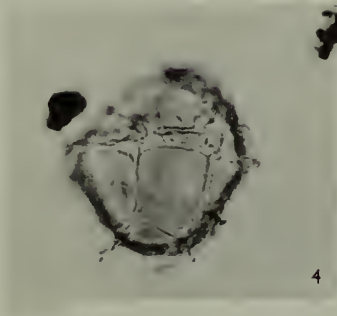
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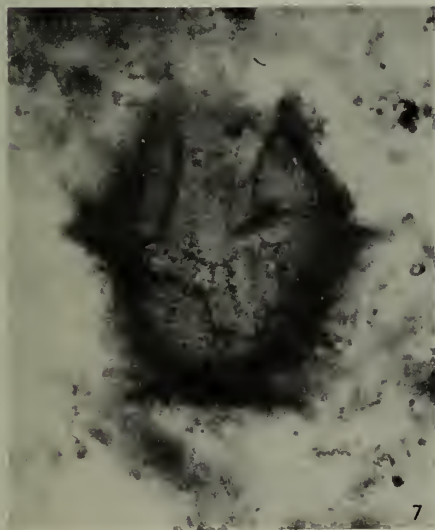
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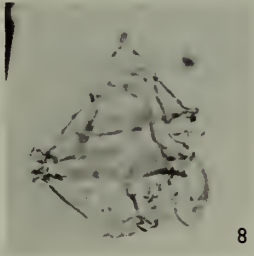
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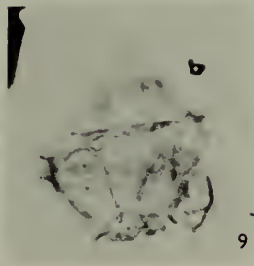
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PLATE 16

Heliodinium patriciae Neale & Sarjeant

FIG. 1. The holotype, V.51710(1), in lateral view. Photographed by phase contrast. $\times 500$.

Heliodinium voighti Alberti

FIG. 2. Ventral surface of specimen, PF.3035(4). $\times 500$.

Microdinium cf. *ornatum* Cookson & Eisenack

FIG. 3. A rather large specimen, oblique ventral view. $\times 500$.

FIG. 4. The same specimen in oblique dorsal view, by transparency. $\times 500$.

FIG. 5. Ventral surface of specimen, PF.3050(1). $\times 500$.

FIG. 6. Dorsal surface of same specimen, viewed by transparency. $\times 500$.

Hystrichodinium pulchrum Deflandre

FIG. 7. Dorsal view of specimen V.51737(1). $\times 500$.

FIG. 8. Lateral view of specimen, V.51737(2), showing archaeopyle. $\times 500$.

Microdinium setosum sp. nov.

FIG. 9. Ventral surface of holotype, PF.3046(2). $\times 500$.

FIG. 10. Dorsal surface of same, viewed by transparency. $\times 500$.

Xiphophoridium alatum (Cookson & Eisenack)

FIG. 11. Antapical view of specimen. PF.3051(1). $\times 500$.

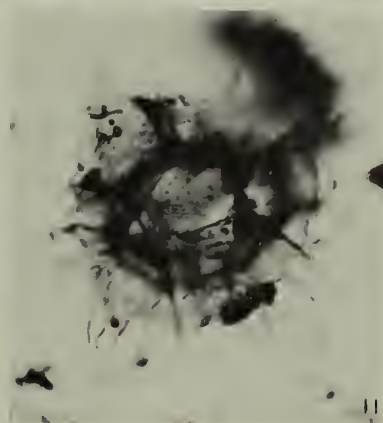
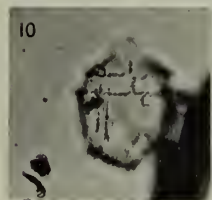
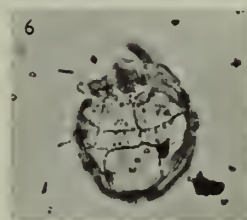
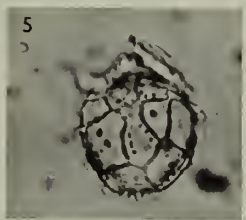
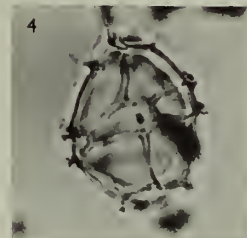
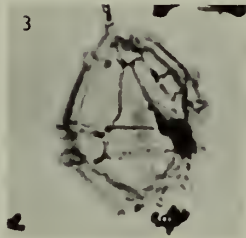
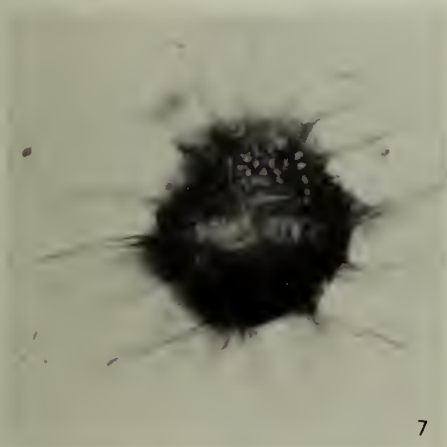
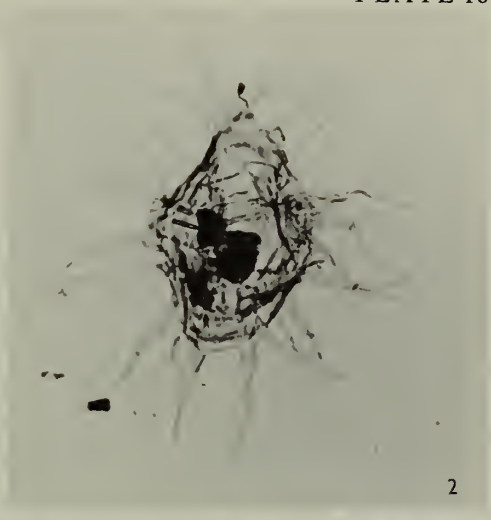
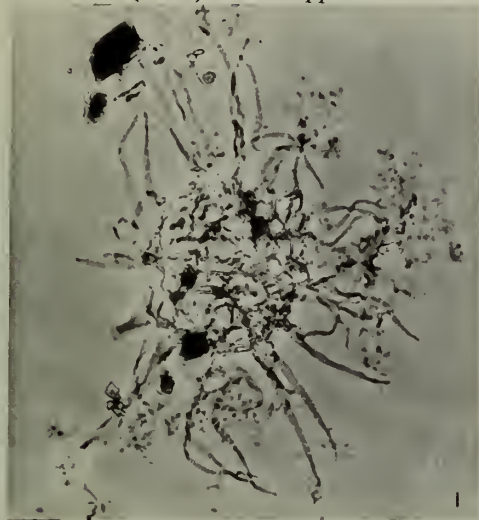


PLATE 17

Hystrichokolpoma eisenacki sp. nov.

FIG. 1. Specimen showing the long antapical process, the slender equatorial processes and the deep sulcal notch. V.51753(2). $\times 660$.

FIG. 2. Holotype, V.51958(1). $\times 660$.

FIG. 3. Specimen with apical plates in position. V.51752(4). $\times 400$.

Hystrichokoploma rigaudae Deflandre & Cookson

FIG. 4. Precingular, equatorial, and postcingular and antapical processes are clearly visible. V.51757(2). $\times 400$.

Hystrichokolpoma eisenacki var. *turgidum* nov.

FIG. 5. Holotype. V.51959(1). $\times 400$.

Hystrichokolpoma unispinum sp. nov.

FIG. 6. Specimen with all processes buccinate. V.51960(1). $\times 660$.

FIG. 7. Holotype. Apical view, sulcus marked by belt of small pores at top left. V.51961(1). $\times 660$.

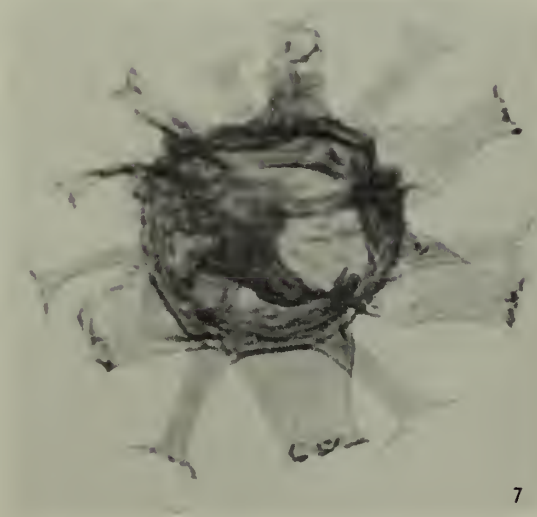
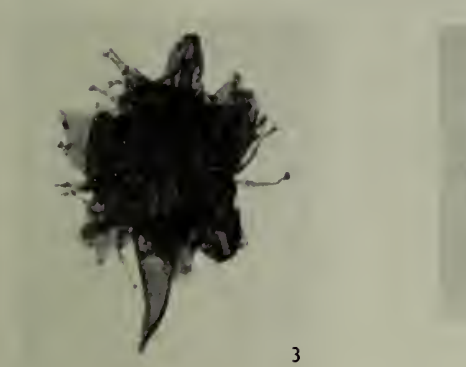
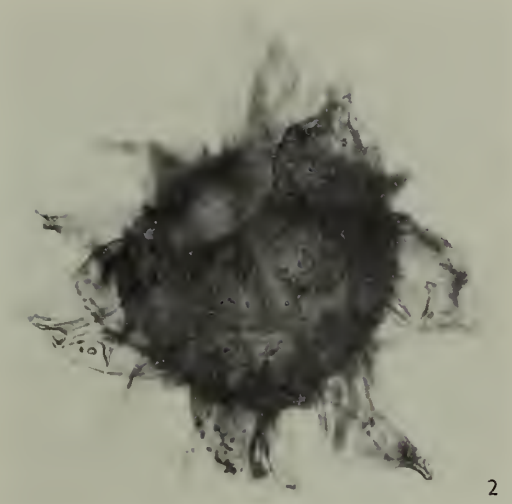


PLATE 18

Wetzelietta (Wetzelietta) articulata Eisenack

FIG. 1. Specimen dorsal side uppermost showing archaeopyle, dorsal view. V.51955(2).
× 330.

FIG. 2. Specimen, ventral side uppermost. V.51961(1). × 330.

FIG. 3. Isolated periphragm operculum from archaeopyle of outer shell. Processes, except for central use, arranged in simulate complexes. V.51763(2). × 700.

FIG. 4. Isolated endophragm operculum from archaeopyle of inner body. V.51763(2).
× 700.

Wetzelietta (Wetzelietta) articulata var. *conopia* nov.

FIG. 5. Specimen, dorsal side uppermost, with periphragm archaeopyle. Slightly displaced. V.51962. × 330.

Wetzelietta (Wetzelietta) clathrata Eisenack

FIG. 6. Narrow strips of minutely perforate membrane connect the distal ends of the processes. V.51958(2). × 330.

Wetzelietta (Wetzelietta) homomorpha var. *quinquelata* nov.

FIG. 7. Specimen showing restriction of processes on the dorsal side to the simulate complexes.Periphragm operculum slightly displaced. V.51963(1). × 330.

Wetzelietta (Wetzelietta) coleothrypta sp. nov.

FIG. 8. Holotype. Ventral view. V.51753(3). × 330.

FIG. 9. Specimen with more numerous spines. V.51964(1). × 330.

Wetzelietta (Wetzelietta) ovalis Eisenack

FIG. 10. Dorsal view of specimen with operculum slightly displaced. V.51965(1). × 330.

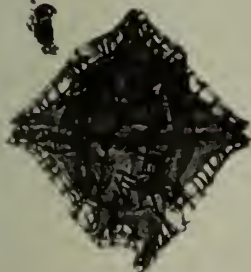


PLATE 19

Wetzeliiella (Wetzeliiella) tenuavirgula var. *crassoramosa* nov.

FIG. 1. Ventral view showing the simulate process complexes of plates 1', 11" and 7". V.51966. $\times 1000$.

FIG. 5. Dorsal view showing simulate complex of intercalary plate 2a, with thick linking bars. V.51966. $\times 1000$.

FIG. 7. Ventral view, archaeopyle seen through ventral surface. Holotype. V.51954(2). $\times 500$.

Wetzeliiella (Wetzeliiella) tenuivirgula sp. nov.

FIG. 2. Dorsal view of holotype with archaeopyle V.51964(2). $\times 330$.

FIG. 4. Dorsal view showing periphragm archaeopyle formed by loss of plate 2a. Simulate complexes of plate 1a, 3a, 4" and 5" surround it. V.51752(5). $\times 1000$.

Wetzeliiella (Wetzeliiella) reticulata sp. nov.

FIG. 3. Ventral view of holotype. V.51752(6). $\times 330$.

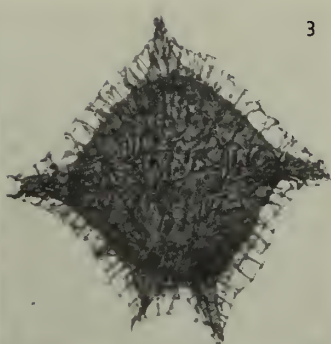
FIG. 6. Stimulate complex of plate 1' and adjacent plates, showing distal network. V.51752(6). $\times 1000$.



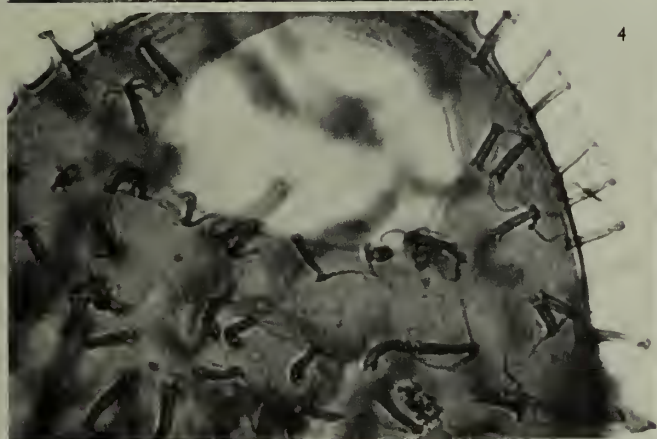
1



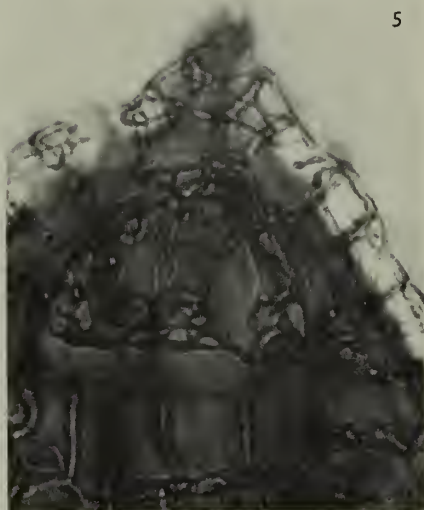
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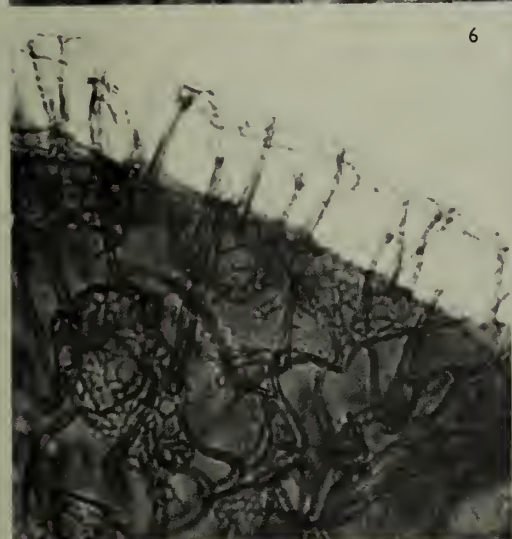
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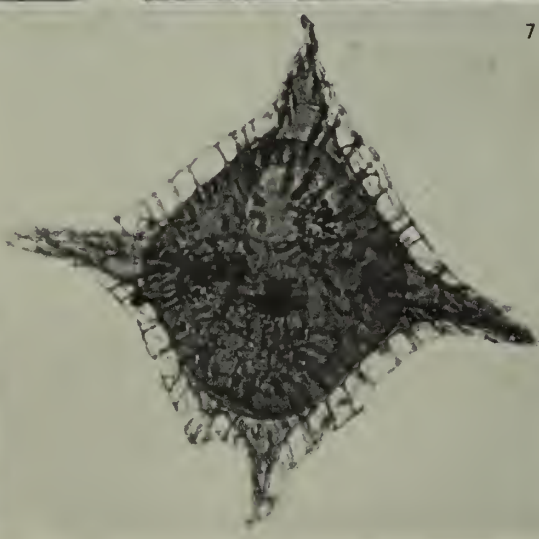
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PLATE 20

Wetziella (Wetziella) condylos sp. nov.

FIG. 1. Ventral view of holotype. V.51967. $\times 500$.

FIG. 2. Specimen with no apical horn. V.51752(7). $\times 500$.

Wetziella (Wetziella) symmetrica var. *lobisca* nov.

FIG. 3. Ventral view. V.51970. $\times 330$.

Wetziella (Wetziella) varielongituda sp. nov.

FIG. 4. Holotype. Dorsal view, with operculum slightly displaced. V.51973. $\times 330$.

FIG. 8. Dorsal view, operculum inside inner body. V.51971. $\times 330$.

Wetziella (Wetziella) similis Eisenack

FIG. 5. Specimen with pyrite crystals concentrated in the horns. V.51969. $\times 330$.

Wetziella (Wetziella) symmetrica Weiler

FIG. 6. Dorsal view. V.51974. $\times 330$.

Wetziella (Wetziella) solida (Gocht)

FIG. 7. Specimen with operculum lying within the central body. V.51968. $\times 330$.

Wetziella (Rhombodinium) glabra Cookson

FIG. 9. Specimen with periphragm operculum in place. V.51958(3). $\times 500$.

FIG. 10. Specimen with operculum missing. Periphragm has been colonized by fungi. V.51972. $\times 500$.

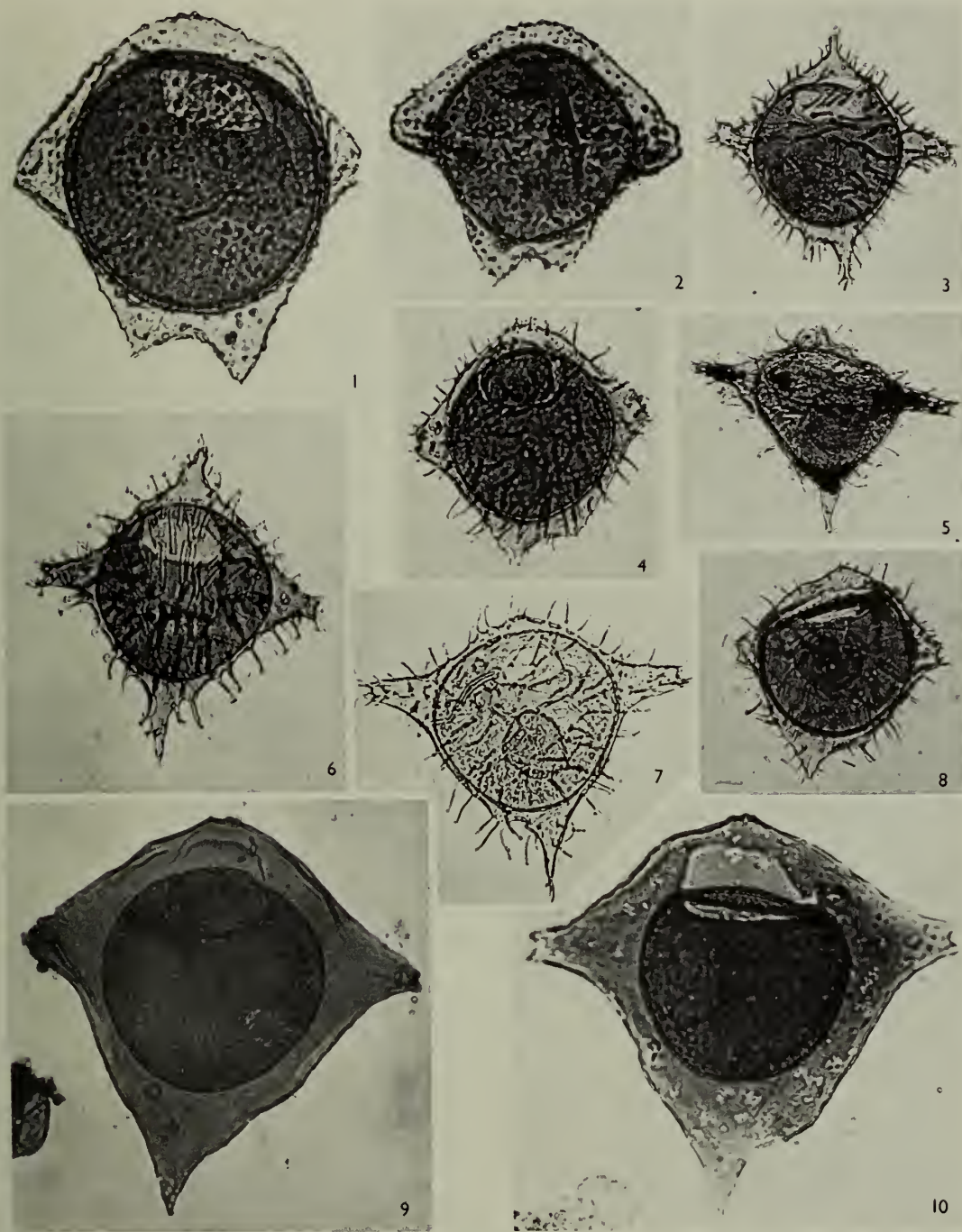


PLATE 21

?*Broomea longicornuta* Alberti

FIG. 1. Specimen V.51733(1). ×500.

Odontochitina operculata (O. Wetzel)

FIG. 2. Specimen V.51730(4). ×c.400.

?*Dingodinium albertii* sp. nov.

FIG. 3. Holotype, V.51719(2). ×500.

Gardodinium eisenacki Alberti

FIG. 4. Specimen V.51726(1). ×500.

Paranetrelytron strongylum gen. et sp. nov.

FIG. 5. Holotype, V.51722(1). ×500.

Muderongia staurota sp. nov.

FIG. 6. Holotype, V.51724(3). ×650.

FIG. 7. Paratype, V.51718(3). ×650.

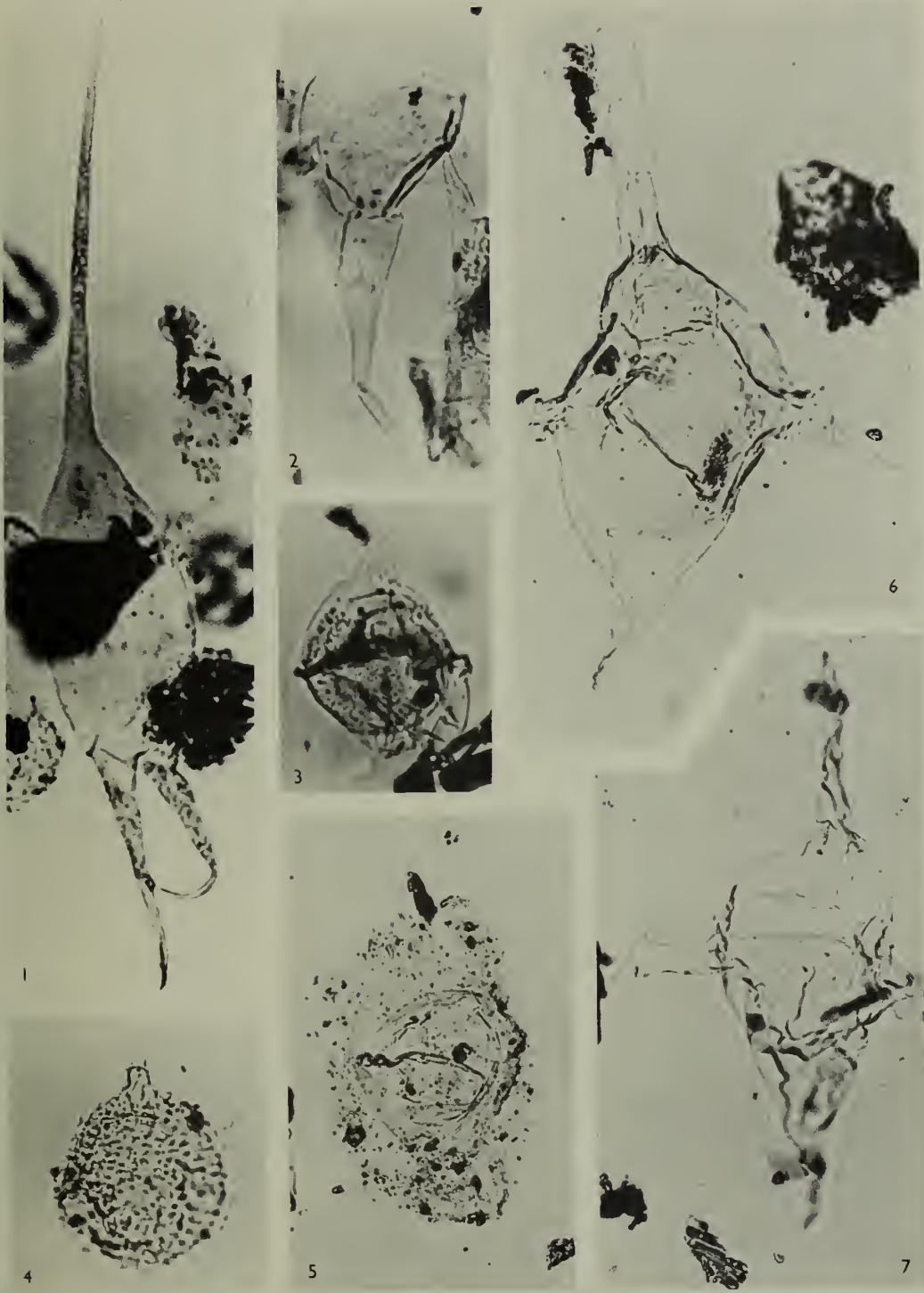


PLATE 22

- Apteodinium maculatum* Eisenack & Cookson
FIG. 1. Specimen V.51718(4). $\times 650$.
- Heslertonia heslertonense* (Neale & Sarjeant)
FIG. 2. Specimen V.51724(2). $\times 500$.
- Netrelytron trinetron* sp. nov.
FIG. 3. Holotype, V.51729(1). $\times 650$.
- Fromea amphora* Cookson & Eisenack
FIG. 4. Specimen V.51732(1). $\times 500$.
- Systematophora schindewolfi* (Alberti)
FIG. 5. Specimen V.51721(1). $\times 500$.
- Cometodinium* sp.
FIG. 6. Specimen V.51723(2). $\times 500$.
- Sirmiodinium grossi* Alberti
FIG. 7. Specimen V.51722(2). $\times 500$.
- Doidyx anaphrissa* gen. et sp. nov.
FIG. 8. Holotype, V.51723(3). $\times 750$.

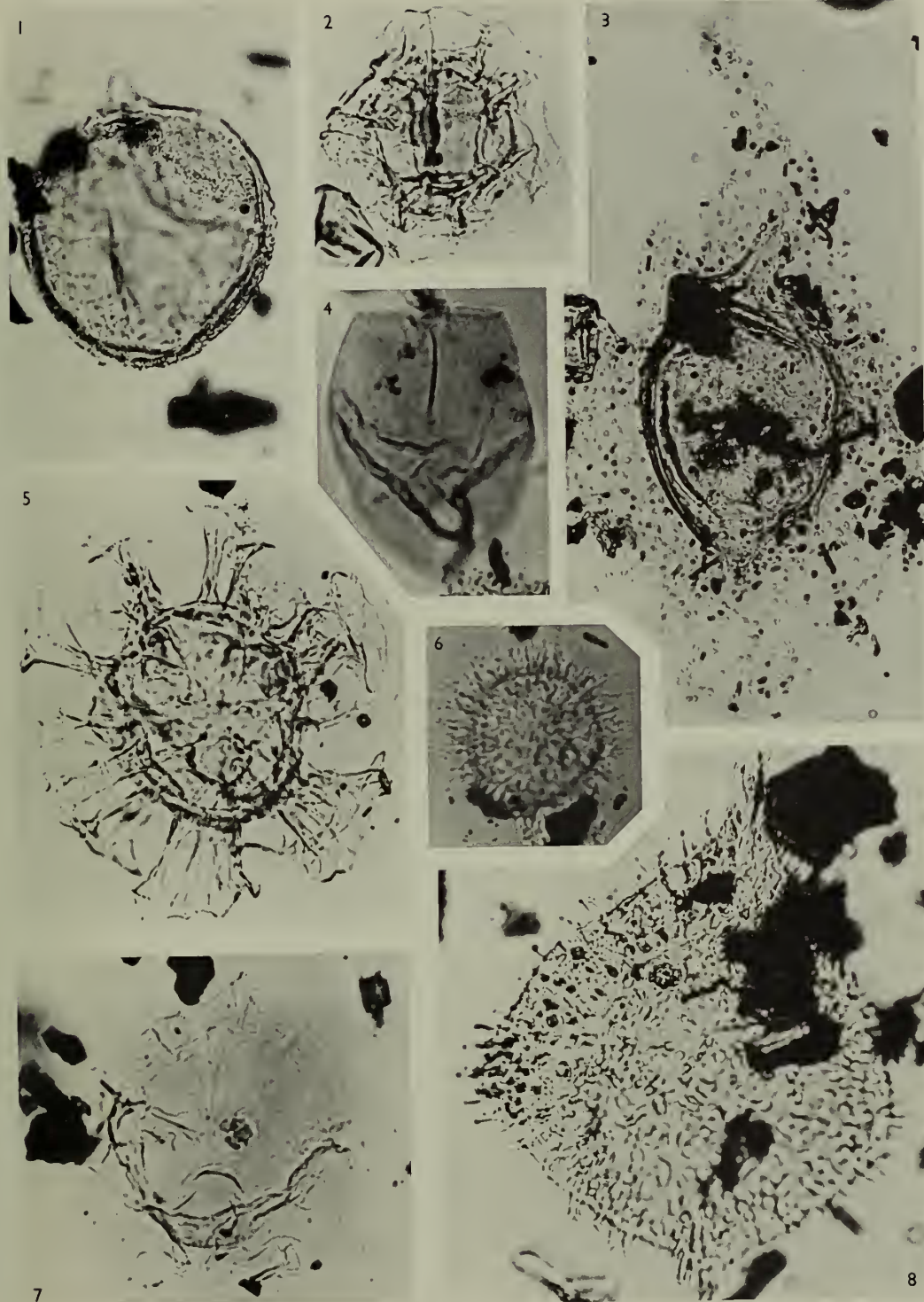


PLATE 23

?Dingodinium albertii sp. nov.

FIG. 1. Holotype, V.51719(2), highly magnified to show the tubercles. $\times c.1250$.

Pareodinia ceratophora Deflandre

FIG. 2. Specimen V.51724(4). $\times 500$.

Fromea amphora Cookson & Eisenack

FIG. 3. Specimen V.51732(2). $\times 500$.

Muderongia staurota sp. nov.

FIG. 4. Specimen V.51724(5), lacking the apex as a result of archaeopyle formation.

Paranetrelytron strongylum gen. et sp. nov.

FIG. 5. Holotype, V.51722(1), photographed by phase contrast at high magnification to show the separation of endophragm from periphragm. $\times c.1250$.

Doidyx anaphrissa gen. et sp. nov.

FIG. 6. Specimen V.51720(1), lacking the apex as a result of archaeopyle formation. $\times 500$.

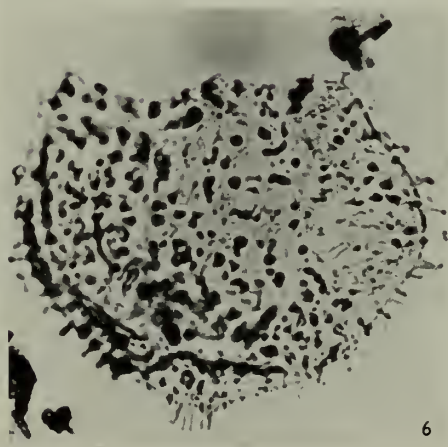
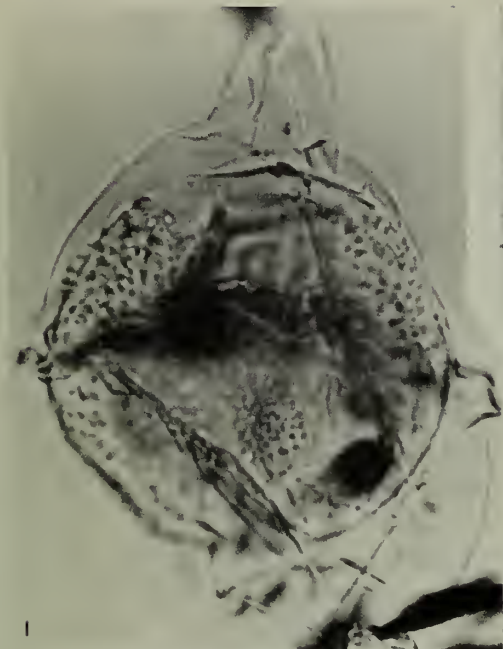


PLATE 24

?Adnatosphaeridium patulum sp. nov.

FIG. 1. Specimen with archaeopyle. V.51975(2). $\times 330$.

FIG. 2. Holotype Complete specimen. V.51977(1). $\times 330$.

Adnatosphaeridium vittatum gen. et sp. nov.

FIG. 3. Complete specimen. V.51753(4). $\times 500$.

FIG. 7. Holotype with apical archaeopyle. V.51976(1). $\times 500$.

Membranilarnacia reticulata sp. nov.

FIG. 4. Holotype. V.51959(2). $\times 500$.

FIG. 6. Specimen with apical archaeopyle. V.51754(2). $\times 500$.

Adnatosphaeridium multispinosum sp. nov.

FIG. 5. Specimen with apical archaeopyle. V.51975(1). $\times 660$.

Cannosphaeropsis reticulensis Pastiels

FIG. 8. Complete specimen. V.51964(3). $\times 500$.

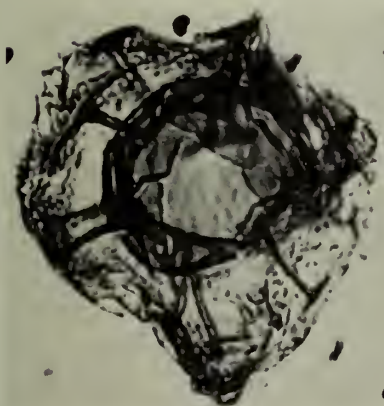
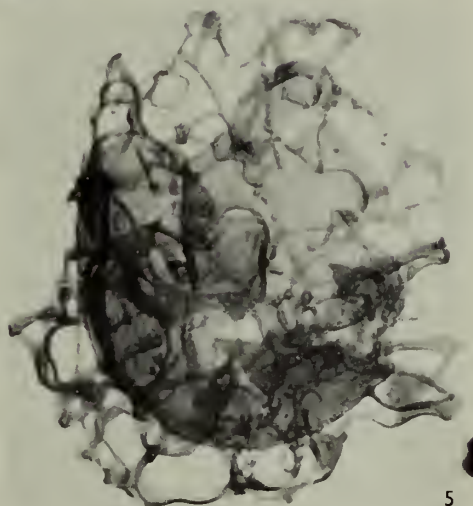
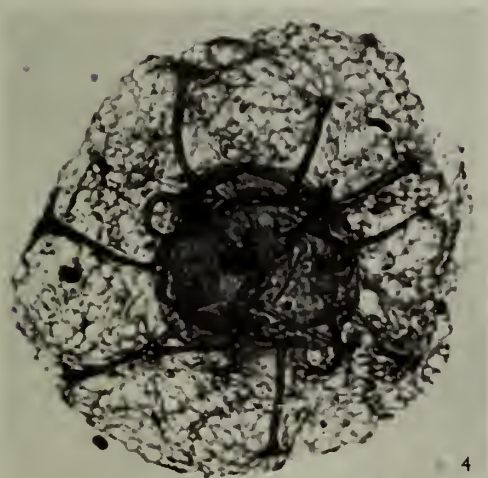
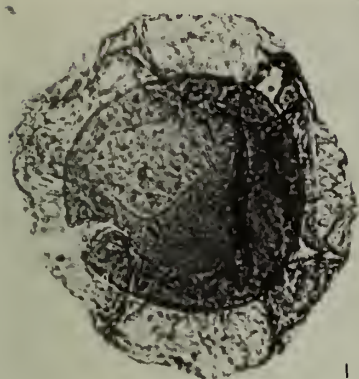


PLATE 25

Cyclonephelium divaricatum sp. nov.

FIG. 1. Specimen with apical archaeopyle and processes on all plates, V.51956(2). $\times 500$.

Cyclonephelium pastielsi Deflandre & Cookson

FIG. 2. Specimen with operculum in place. V.51978(1). $\times 500$.

Cyclonephelium ordinatum sp. nov.

FIG. 3. Dorsal view of specimen with apical archaeopyle. V.51977(2). $\times 330$.

Areoligera cf. *medusettiformis* (O. Wetzel)

FIG. 4. Dorsal view of specimen with apical archaeopyle, note sulcal notch on the right of the mid-ventral line. V.51746(3). $\times 660$.

Areoligera cf. *coronata* (O. Wetzel)

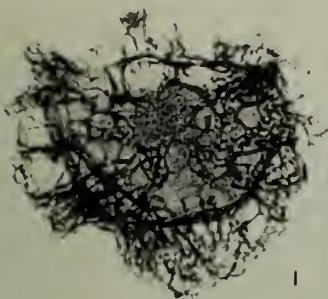
FIG. 5. Specimen showing the soleate process complexes on the ventral surface. V.51756(4). $\times 660$.

Areoligera cf. *senonensis* Lejeune-Carpentier

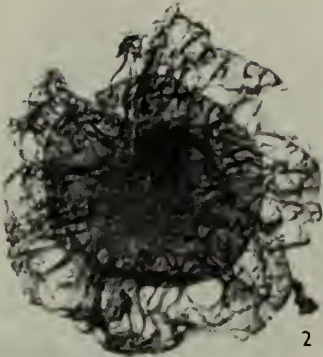
FIG. 6. Complete specimen. V.51757(3). $\times 660$.

Areoligera coronata (O. Wetzel)

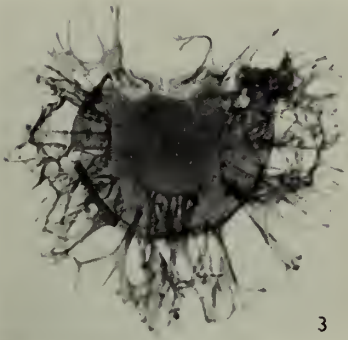
FIG. 7. Dorsal view. Processes arranged in soleate complexes, apical archaeopyle. V.51959(3). $\times 500$.



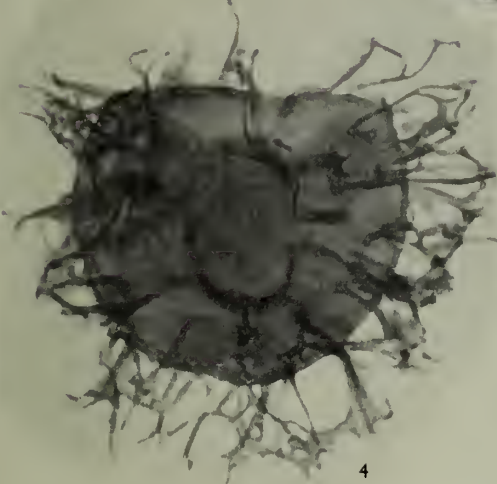
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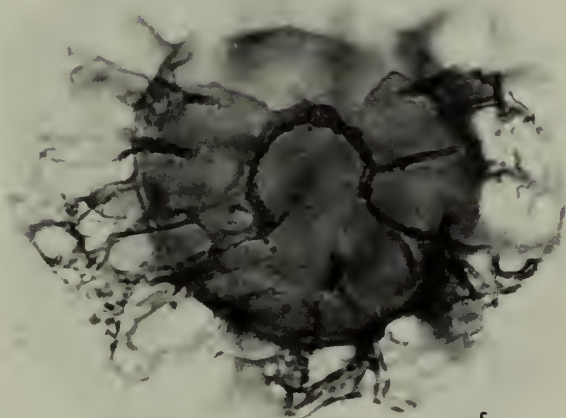
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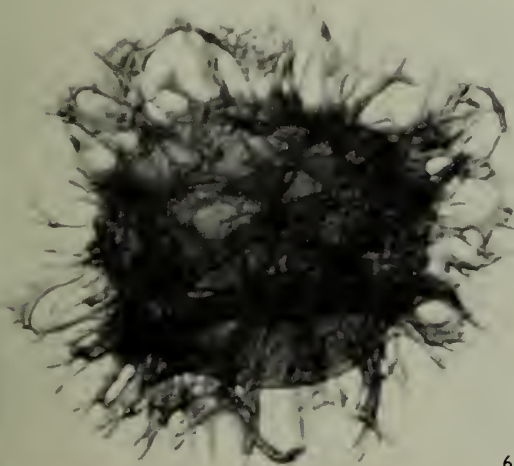
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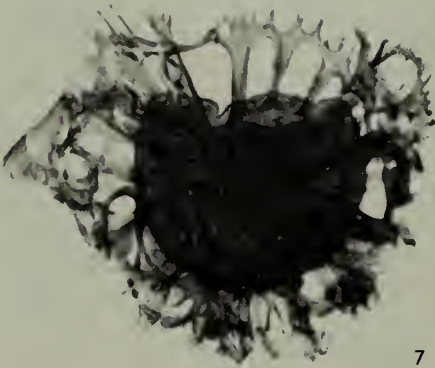
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PLATE 26

Deflandrea oebisfeldensis Alberti

FIG. 1. Specimen with endrophragm operculum slightly displaced. V.51979. $\times 400$.

Deflandrea phosphoritica subsp. *phosphoritica* Cookson & Eisenack

FIG. 2. Specimen with no inner body, periphragm operculum lying inside. V.51753(5). $\times 400$.

FIG. 3. Specimen showing girdle and slightly displaced periphragm operculum. V.51955(3). $\times 400$.

FIG. 6. Specimen with a "decomposed" inner body. V.51752(8). $\times 400$.

FIG. 9. Specimen with archaeopyle. V.51747(3). $\times 400$.

Deflandrea phosphoritica subsp. *australis* Cookson & Eisenack

FIG. 4. Complete specimen. V.51752(9). $\times 400$.

Deflandrea wardensis sp. nov.

FIG. 5. Holotype with archaeopyle. V.51980(1). $\times 400$.

Thalassiphora pelagica (Eisenack)

FIG. 7. An operculum is visible. V.51757(4). $\times 240$.

Thalassiphora delicata sp. nov.

FIG. 8. Holotype. V.51756(3).

